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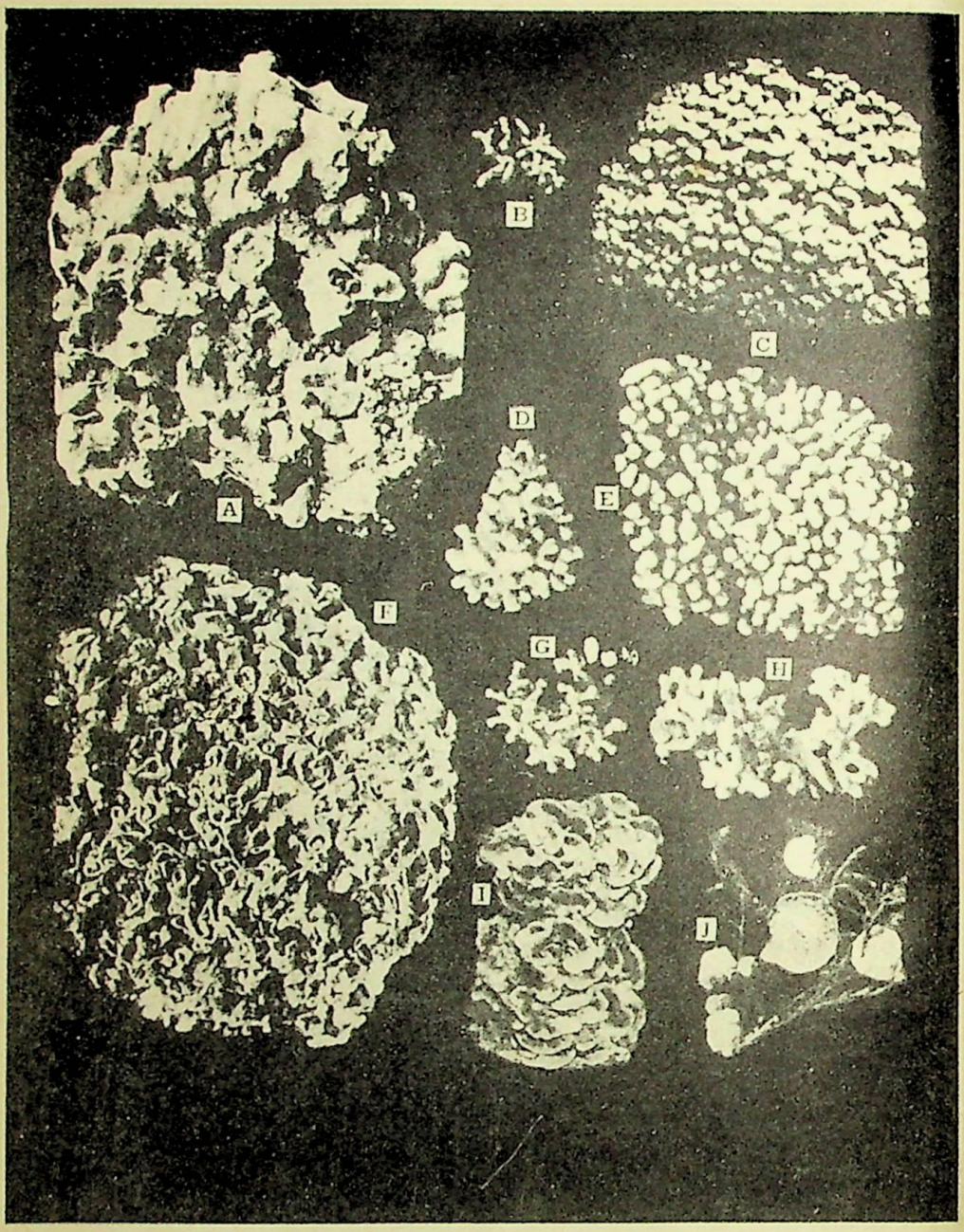

Frontispiece. Habits of Melobesieae (after Foslie). A, *Lithophyllum expansum* Phil. f. *stictaeformis* (Aresch.) Foslie. B, G, *Lithothamnion calcareum* (Pall.) Aresch. f. *coralloides* (Crn.) Foslie. C, *L. glaciale* Kjellm. f. *subfastigiata* Foslie. D, *L. indicum* Foslie. E, *L. colliculosum* Foslie. F, *L. lichenoides* (Ell. & Sol.) Foslie f. *agariciformis* (Johnst.) Foslie. H, *L. calcareum* (Pall.) Aresch. f. *compressa* (Mc Calla) Foslie. I, *L. lichenoides* (Ell. & Sol.) Foslie f. *depressa* Foslie. J, *L. Patena* (Hook. & Harv.) Heydr.

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THE STRUCTURE AND REPRODUCTION OF THE ALGAE

VOLUME II

Foreword, Phaeophyceae, Rhodophyceae, Myxophyceae

BY

F. E. FRITSCH

84682

पुस्तकालय

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गुरुकुल कांगड़ी विश्वविद्यालय

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PREFACE TO VOLUME II

The considerable delay in the appearance of this volume resulted from a variety of circumstances which were beyond my control. The manuscript was finally completed in September 1941, and any further delay in publication is due to the difficulties of the present situation. So far as it has been possible to obtain access to non-British periodicals, the current literature has been included up to the middle of 1943, the additional references being incorporated at the end of the main lists as in the first volume. In the frequent cross-references made to the subject-matter of that volume, it is always cited merely by the Roman numeral I.

During the preparation of the sections dealing with the Brown and Red Seaweeds it became evident that a brief preliminary survey of their conditions of life and of their distribution in nature would not only be helpful in relation to the later matter, but would also prevent a certain amount of repetition. With these objects in view I have prefixed the subject-matter of the present volume with a Foreword. A more exhaustive consideration of the topics dealt with in these preliminary pages was not feasible without unduly increasing the size of the book. Apart from this, the general treatment follows the same lines as in the first volume. In view, however, of the numerous synonyms (of which only the more essential have been mentioned), these have been specially indicated in the index.

I have again to acknowledge the valuable help afforded by Oltmanns' *Morphologie und Biologie der Algen*. Special mention should also be made of C. Sauvageau's numerous researches on Phaeophyceae, of P. Kuckuck's, L. Kolderup Rosenvinge's, and H. Kylin's many memoirs on Phaeophyceae and Rhodophyceae, and of L. Geitler's contributions on Myxophyceae. A considerable number of the illustrations in this volume have been taken from the published works of these scientists who have contributed so much to the advancement of our knowledge of the three classes with which it deals. I am also greatly indebted to the University of Michigan Press and to Prof. W. Randolph Taylor for permission to make use of a considerable number of illustrations[1] from the latter's *Marine Algae of the Northeastern Coast of North America*. I am similarly indebted to the Trustees of the British Museum, London, for permission to reproduce figs. 18 B, 19 C, 27 A, 35 A, 36 A and I, 60 E, 81 A, 91 C and F, 118 D, 154 A, 163 C, 170 B and C, 176 D, 186 H and 192 A from L. Newton's *Handbook of the British Seaweeds*, and to

[1] All of those cited as "after Taylor" with the exception of figs. 24 C and 109 A are from this source.

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the University Press, Liverpool, for fig. 117 A taken from M. Knight's and M. W. Parke's *Manx Algae*. A few illustrations (figs. 83 A, 111 F, 130 A and B, 163 A) are reproduced from the work of Oltmanns cited above, although current events have not admitted of obtaining sanction for their reproduction; it was, however, difficult, if not impossible, to find substitutes of a comparable degree of excellence. The photograph of *Ecklonia buccinalis* (fig. 79 A) was kindly sent me by Dr M. A. Pocock. Mr R. Cullen has again afforded invaluable help in the photographic reproduction of the illustrations and has spared no pains to obtain the best results.

I am greatly obliged to Dr F. M. Haines, who has read through all the sections dealing with physiological topics, and to Prof. E. G. Pringsheim who gave me the benefit of his criticism of the section dealing with Blue-green Algae. I am glad to have this opportunity of expressing my gratitude to the staff of the University Press for their important contribution towards the success of the two volumes.

In concluding this work, which has taken up the major part of my leisure time during a period of fifteen years, I venture to express the hope that it will fulfil its purpose of giving an indication of what is known about the structure and reproduction of the Algae and of stimulating enquiry in the many directions in which our knowledge of these matters is inadequate.

F. E. FRITSCH

CAMBRIDGE
February 1943

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FOREWORD

A large part of this volume deals with those classes of Algae that play a dominant rôle in the vegetation of the sea, and it is therefore appropriate to commence with a brief consideration of the conditions of life and distribution of seaweeds. By contrast to fresh-waters most seas afford two distinct habitats for the attached flora, viz. (*a*) the part of the shore that is twice daily covered and uncovered by the tides, and (*b*) the more extensive region below low-water mark in which the algal vegetation always remains submerged. These regions, first designated *littoral* and *sublittoral* respectively by Kjellman((69) p. 57, (70)), manifestly offer different conditions of existence for the seaweed population.[1]

That of the littoral region, which is usually taken as extending down to the limit of neap tides, must be capable of surviving periods of exposure of varying duration, involving desiccation and insolation, with accompanying alterations in temperature, salt-concentration, hydrogen-ion-concentration, etc. The density of the population on rocky shores, especially in temperate seas, is testimony to the ability of littoral seaweeds to withstand the effects of diurnal exposure, the intensity of which progressively increases as high-tide level is approached. The vertical range of the algal covering may, however, especially on exposed shores, extend to appreciably above even spring-tide level, where the only source of sea-water is afforded by spray during rough weather. All attempts to define this *spray-zone* more accurately have failed (cf. (10) p. 709, (24) p. 14, (83) p. 66), and it is nowadays usually included in the littoral region.

Many workers emphasise that the capacity of littoral, as contrasted with sublittoral, seaweeds to resist desiccation is one of the principal factors determining their existence in the intertidal zone ((37) p. 41, (46) p. 116, (51), (58), (59), (63) p. 325, (101) p. 579, (103), (104)); Kaltwasser (66) has investigated the effects of this factor on respiration and photosynthesis. Desiccation is, however, not the only consequence of exposure. Littoral seaweeds must be able to withstand temperature-changes, involving in the higher latitudes subjection to frost during winter and strong insolation during summer (cf. (5) p. 390, (7), (70) p. 11, (99) p. 829, (102), (118) p. 15, (160) p. 50), the latter factor becoming increasingly potent as the Tropics are approached. The Fucales, as well as other common Algae of the littoral region (*Bangia fusco-purpurea*, species of *Porphyra*, *Chondrus crispus*), have been shown (82) to withstand exposure to low temperatures and *Fucus*, *Porphyra* and *Enteromorpha*

[1] Cf. especially (10) p. 708, (24), (80) p. 208, (81), (83) p. 66, (90) p. 6, (91) p. 120, (96) p. 35, (120), (128) p. 189, (153*a*). Jónsson ((65) p. 80) distinguishes upper and lower littoral zones, the latter comprising the area exposed only at spring tides (cf. also (62) p. 191, (179)).

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are stated to be able to survive temperatures of −20° C. On the other hand diverse Mediterranean Florideae are killed by exposure to 1–2° C. ((7) p. 391). *Bangia fusco-purpurea* and *Urospora penicilliformis* can also withstand high temperatures, and many other littoral Algae are possibly eurythermic forms ((113) p. 359).

The effects of desiccation (cf. (6) p. 359) and of temperature-changes alike become more intense at successively higher levels on the shore, and this is also true of changes in salt-concentration, due either to evaporation or to dilution by rain-water ((63) p. 325, (100), (172)). Seaweeds vary considerably in their capacity to survive immersion in hypo- and hypertonic sea-water ((6) p. 352; cf. also p. 401). Littoral forms, which are completely exposed during low water, can withstand concentrations ranging between 0·2 and 3·0 sea-water, while those which rarely become altogether dry or occupy rock-pools exhibit a more limited range (0·3–2·2); permanently submerged forms, on the other hand, are far more sensitive to concentration changes (range: 0·5–1·4 sea-water; cf. also (9)).

There is also a gradation in the period of exposure to light during low, and in the depth of submergence during high, tide, although the importance of this feature has in recent years been rather discounted ((101) p. 579, (119) p. 70). Movement of the water accelerates respiration and photosynthesis (45), especially in littoral Algae. A useful review of what is known in these respects is given by Biebl (8); see also (190), as well as (141) on the culture of marine Algae.

The often marked zonation of the seaweed population in the littoral region is no doubt a result of the progressive incidence of the exposure factors. It is strikingly demonstrated by the girdles of Fucaceae found on rocky shores in the North Temperate zone (p. 382) and is no less evident in the characteristic communities dominated by Florideae such as *Laurencia pinnatifida*, *Lomentaria articulata*, *Gigartina stellata*, as well as by species of *Gelidium* and *Corallina* in the lower parts of the littoral region (cf. (10) p. 732, (24) p. 33, (46) p. 103, (123) p. 89, (141*a*) p. 337, (142) p. 69). At the upper limit, where the conditions are extreme, zonation is usually most obvious. Characteristic representatives, which occupy more or less clearly marked belts in the upper littoral (incl. the spray-zone) in the North Temperate zone, are species of *Prasiola* (*P. stipitata*) and *Urospora*, *Ulothrix flacca*, *Pelvetia canaliculata*, *Fucus spiralis*, *Porphyra umbilicalis*, *Bangia fusco-purpurea*, *Rivularia atra*, and *Calothrix scopulorum*, with which are associated the lichens *Verrucaria* (*V. maura*, etc.) and *Lichina* and, in somewhat more shaded situations, the red alga *Hildenbrandia*. A comparable distribution is observable in the Mediterranean ((37) p. 179, (94) p. 197), and on the Atlantic coast of North America ((62), (166) p. 7). Mention should also be made of the characteristic belts of Chrysophyceae and other Algae found in the spray-zone on the British chalk-cliffs ((1) p. 163) and of the blue-green communities inhabiting the limestone and dolomitic rocks of the Mediterranean (see p. 866).

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In other parts of the world Brown Algae do not play so conspicuous a part in the intertidal belt. Thus, on South African coasts Red Algae predominate ((61) p. 19), in New Zealand the larger Brown Algae (*Carpophyllum*, *Marginariella*, *Xiphophora*, etc.) occur at and below low-tide level ((112) p. 518), while in the Tropics the littoral zone may be occupied by considerable numbers of Florideae ((97) p. 46, (162) p. 200). On the Pacific coasts of North America species of *Endocladia* and *Porphyra perforata* often occupy more or less clearly marked zones near high-tide limit ((104*a*) p. 64), while in South Africa *P. capensis* occurs at this level ((60) p. 145; cf. also (112) p. 526). In the Arctic ((71) p. 9) and Antarctic ((126*a*) p. 183, (156) p. 253) the littoral region is for the most part devoid of vegetation, which is largely the result of ice-action ((27) p. 447, (179) p. 64); the effect often continues into the upper part of the sublittoral ((130) p. 7).

The rock-pools in the intertidal belt ((5) p. 383, (10) p. 735, (20), (47) p. 51, (63), (72), (142) p. 86, (155)) harbour a vegetation which usually differs more or less markedly from that on the rocks around, although varying in character at different levels on the shore; in the deeper pools there may be some vertical zonation. The desiccation factor is lacking, but in the higher pools, which are subjected to prolonged insolation, the water shows marked temperature variations, as well as changes in salt- and hydrogen-ion-concentrations. Photosynthesis of the seaweeds during low tide may result in a *p*H as high as 9·9 (2, 5). Many Algae can, however, exist in *p*H ranges of 6·8–9·6 (84), although Gail (41) concludes that *Fucus evanescens* is killed by a *p*H above 8·7. According to Kylin the younger parts are in general more susceptible than the older to *p*H changes. Sand-covered rocks, as well as sandy pools ((123) p. 83, (177) p. 376), are often occupied by special communities.

In the Baltic, in which there are practically no tides, a littoral region of the type just considered is lacking. On the other hand there is a limited zone that becomes uncovered at certain times of the year, largely as the result of wind-action, and this is nowadays usually defined as the littoral region ((31) p. 93, (32) p. 70, (50) p. 7, (83) p. 85, (91) p. 123, (108) p. 44, (161) p. 22). In certain respects it is more comparable to the periodically uncovered parts of the shore-line of a lake, and the prolonged period of exposure results in the non-survival of the bulk of the vegetation, most of which consists of short-lived annuals.

In the sublittoral region it is essentially quantity ((33) p. 637, (73), (119) p. 55) and quality (see p. 408) of the light that determines the zonation of the seaweed population; such zonation is often plainly shown by the epiphytic growth on the larger submerged Phaeophyceae ((4) p. 422, (10) p. 757). Changes in temperature and salinity with increasing depth are, however, probably sometimes of some significance. The depth to which the sublittoral seaweeds extend

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varies in different latitudes, being for instance much greater in the Mediterranean and other southern seas than in northern ones ((4) p. 414, (134*a*) p. 177). In the upper reaches Brown (especially Laminariales and certain Fucales) and Green Algae still play an important rôle, but in the deeper water Red Algae tend to predominate, although some green and brown forms occur at appreciable depths ((4) p. 473, (37) p. 84, (40) p. 286, (118), (139) p. 480, (164) p. 35, (179) p. 61).

Many sublittoral seaweeds are no doubt shade-forms, with a low compensation point and capable of effective photosynthesis in weak light, whilst the littoral types include many sun-forms ((33) p. 637, (100*a*)). Since, with increase of temperature the rate of respiration rises more rapidly than that of photosynthesis, sublittoral Algae in the warmer seas (especially in summer) will soon reach the compensation point with increasing depth. The fact that the majority of seaweeds on Swedish coasts show vegetative growth in winter and spring is attributed by Printz ((119) p. 58) to a low rate of respiration so that, in spite of the low light-intensity, an assimilatory gain is nevertheless possible (cf. also (34) p. 276, (52) p. 281, (77)). Brown and Green Algae of temperate zones seem in general to be adapted to higher light-intensities than the red forms ((33) p. 636, (34) p. 278), but the increasing importance of the latter in the warmer seas ((37) p. 281, (128) p. 173, (162) p. 199) and even in the littoral zone (cf. above) shows that there must be many Florideae capable of existence in strong light, the distribution of which is determined by other factors. The capacity of shade-forms to utilise and to withstand higher light-intensities varies for representatives of the three chief marine classes (33, 101), green forms markedly surpassing Brown and Red Algae in both respects; deep-water members of these two classes exhibit relatively little increase in photosynthesis at the surface, although Brown Algae are relatively resistant to the stronger illumination. Such facts indicate the great differences in the attunement of marine Algae to intensity of illumination.

Montfort ((101) p. 579) concludes that it is mainly factors other than the quality or quantity of the light that prevent the penetration of the majority of littoral Algae into deeper water and that exclude sublittoral forms from the littoral region. An influence of light-intensity, difficult to dissociate from the higher humidity, is seen in the changed character of the seaweed-flora within caves ((1) p. 174, (10) p. 739, (24) p. 43, (35) p. 220, (80) p. 223, (141*a*) p. 344, (142) p. 83); here the vegetation, apart from harbouring certain characteristic species (*Rhodochorton Rothii* in northern waters), often includes a number of those otherwise found only in the sublittoral region.

The character of the flora, though essentially the same in a given geographical area, exhibits numerous modifications in different habitats and at different seasons of the year (cf. e.g. (52*a*) p. 48). In North Temperate seas and in the Mediterranean the littoral and the

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upper parts of the sublittoral regions are the home of a considerable number of annuals (Ectocarpales, diverse Florideae) which are represented only for a few months so that the richness and character of the vegetation varies with the seasons ((76) p. 12). Moreover, many of the perennials die down to a large extent in winter, only the basal attachment system or the larger axes persisting; many examples of this are given in the course of this volume. Some perennials (*Hildenbrandia*, *Fucus serratus*), however, may exhibit vegetative growth throughout the year ((80) p. 274).

In North Temperate seas the flora is usually at its height in July and August, but a number of littoral seaweeds tend to disappear from between tide-levels with the onset of summer, although they may survive in the lower part of the littoral or sublittoral as the case may be ((76) p. 27, (123) p. 130); in other instances the distribution may be reversed (122). Similar, but more marked "migrations" are recorded for the Mediterranean ((4) p. 422), where the littoral vegetation, which is at its best during winter and spring (cf. also (112*a*) p. 71), becomes strongly reduced in summer when the sublittoral flora reaches a maximum. It can scarcely be doubted that the varying intensity of illumination over the year is the most important, although not the only, factor concerned. In the Arctic, where growth is most vigorous during spring and summer, there are scarcely any annuals ((10) p. 828, (71), (128) p. 239), while the littoral region of the Tropics is rich in perennials ((162) p. 218).

Various schemes have been advanced for the ecological grouping of marine Algae. Those of Oltmanns ((115) p. 298), Funk ((40) p. 220), and Gislén ((47) p. 84) are based essentially on external form and, while this no doubt gives some index of the biological conditions, it cannot be regarded as affording a basis for a true ecological classification. The schemes proposed by Setchell ((151) p. 30, (152) p. 310) and Feldmann ((37) p. 137) take a wider cognisance of the conditions of life, and the latter in particular endeavours to found a classification, analogous to that of Raunkiaer for land-plants. Setchell's grouping is based principally on the conditions of illumination and the degree of exposure to wave-action, while that of Feldmann refers especially to the duration of life and the form in which the seaweed survives the dormant season. Among annuals he distinguishes Eclipsiophytes (persisting as minute filamentous growths, many Ectocarpales) and Hypnophytes (with dormant reproductive stages, e.g. *Vaucheria piloboloides*); among perennials Phanerophytes (entire thallus persisting, *Codium*, *Halimeda*), Chamaephytes (encrusting forms, *Hildenbrandia*, *Melobesia*), Hemiphanerophytes (only part of erect thallus persisting, *Cystoseira*, *Sargassum*, *Sphaerococcus*), and Hemicryptophytes (only basal portion persisting, *Acetabularia*, *Cladostephus*, *Rissoella*). It must be noted, however, that exposure is a factor that enters only into the conditions of life in the littoral region. Moreover, the concepts of annual and perennial as applied to seaweeds are somewhat elastic, since the same

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species may behave as an annual in one and as a perennial in another geographical area (cf. (10) p. 826), or be annual in the littoral and perennial in the sublittoral region (cf. (139) p. 485).

Data on the time of reproduction of seaweeds (cf. e.g. (10) p. 829, (18), (49) p. 144, (65) p. 172, (76), (80) p. 244, (93), (118), (121); and for the Mediterranean (40)) tend to show that the same species exhibits considerable variety in this respect in different regions.

Since most seaweeds are lithophytes or epiphytes on the larger rock-inhabiting forms (especially Laminariales and Fucales), a rocky coast-line alone affords the substrata necessary for the development of a rich algal vegetation. Sandy or shingly shores are relatively poor, although a special facies is often developed on the mud-flats of salt-marshes ((15), (16), (17) p. 185; see pp. 383, 862). Even on rocky shores the abundance and composition of the algal flora depend to a considerable degree on the extent of wave-action ((10) p. 693, (24) p. 19, (91) p. 132, (123) pp. 75, 81, (184) p. 367); certain of the littoral Fucales, for instance, may be lacking or little represented where there is marked exposure to this influence ((24) p. 24; see p. 382). The angle of slope of the rock also affects the distribution of Brown Algae ((68) p. 694, (123) p. 86, (184)).

Biotic factors no doubt play a considerable rôle, although relatively little information is as yet available on this point. There is marked competition for a suitable substratum ((76) p. 28, (136) p. 21), although the stages in colonisation of new surfaces by littoral Algae are as yet little studied ((27) p. 477, (67), (124), (174), (182)). Plant and animal communities also compete with one another ((123) p. 80, (124) p. 431, (127)). Diverse Molluscs *inter alia* attack and devour seaweeds, especially the germlings,[1] while Chemin ((19) p. 360) states that the carpospores of Red Algae are very liable to be devoured by Infusoria.[2]

Many land-locked seas fed by large rivers contain a smaller proportion of dissolved salts and of these the Baltic has been extensively studied. The effects on the vegetation are many. There is a considerable reduction in the number of species (cf. also (175) p. 112, (179) p. 6), and certain of these are represented by reduced forms of smaller stature and usually of narrower dimensions ((80) p. 246, (91) p. 141, (131) p. 42, (161) p. 12, (183)), although it is possible that special races are involved. Certain Chlorophyceae, as well as *Pylaiella rupincola*, *Sphacelaria racemosa*, etc., however, appear to be unaffected. The strongly dwarfed

[1] See (3), (16) p. 216, (18) p. 85, (78), (79) p. 151, (98) p. 28, (116), (135), (137) p. 12, (168) p. 159, (171*a*) p. 60.

[2] The relative distribution of fauna and seaweeds at different levels in the littoral region is dealt with by Colman ((23); cf. also (47) p. 87, (184) p. 362, (186)). Regarding the algal growth often found on the carapace of crabs, see (64) and the literature there cited. With reference to the relation between the algal vegetation and the general productivity of the sea, see (42) p. 36, (95), (117), (181). As regards economic uses, see (22) p. 8, (24) pp. 53, 151, (29), (36) p. 9, (54) p. 31, (96) p. 47, (97) p. 43, (143) p. 102, (145) p. 189, (158), (159), (180).

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forms are always sterile, but even when there is only a moderate degree of reduction reproductive organs are less abundant. Many workers ((30), (48), (74), (85) p. 245, (113) p. 377, (114) p. 39, (167)) have investigated the effect of reduced salinity on marine Algae, but its influence on essential physiological processes has only recently been studied. Legendre (89) records increased photosynthesis in *Fucus serratus* and *Ulva Lactuca*, although Fromageot (39) in the latter established a decrease. According to Hoffmann ((55) p. 261) a lowered salt-concentration increases respiration in *Fucus serratus* and *Laminaria digitata*, although *F. vesiculosus*, *Enteromorpha* and *Porphyra* are unaffected. The scanty data imply that in water of reduced salinity diverse seaweeds will reach the compensation point more rapidly.

THE GEOGRAPHICAL DISTRIBUTION OF SEAWEEDS

The ensuing account of geographical distribution is intended as an introduction to the topic and makes no claim to be complete. The local variations in the flora are on the whole insignificant when compared with the marked diversities which are encountered in different parts of the world. Thus, the algal populations of the Old and New Worlds and of the Northern and Southern Hemispheres present numerous points of contrast, while that of the Atlantic is in large part distinct from that of the Indian and Pacific Oceans. A certain number of marine Algae enjoy a wide geographical distribution (e.g. *Digenea simplex* in all warmer seas), while some would appear to be almost cosmopolitan (*Ulva Lactuca*, *Colpomenia sinuosa* (?), *Ectocarpus siliculosus*, *Sphacelaria furcigera*, *Melobesia farinosa*, *Catenella Opuntia*, *Gracilaria confervoides*, *Hypnea musciformis*), but the vast majority are restricted to definite, though often relatively wide, areas. For most seaweeds the warm water of the equatorial belt constitutes an impenetrable barrier, and *Scytosiphon Lomentaria*, for instance, although recorded from the colder regions of both the Northern and Southern Hemispheres, is lacking in the Tropics (cf. also (44) p. 150, (107)).

Temperature ((54) p. 20, (75) p. 123, (87) p. 307, (105) p. 169, (113) p. 355) is no doubt one of the principal factors determining the latitudinal distribution of marine Algae, a view specially advanced by Setchell. He showed (144) that the distribution of the genera of Laminariales (cf. p. 253) is markedly related to the mean maxima for the hottest months and that it coincides with the isotheres of 10°, 15°, 20° and 25° C. Later (146, 147) Setchell draws attention to the importance of the mean minima of the surface-waters and suggests (148, 149) that the temperature-interval between the mean minima and maxima (as a rule probably about 10° C.) may determine whether reproduction can take place and therefore whether survival is possible. He distinguishes (146, 148) nine climatic zones (Boreal, Upper Boreal, North Temperate, North Subtropical, Tropical, South Subtropical,

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South Temperate, Upper Austral, Austral), determined by temperature-intervals (surface-isotheres) of 5° C., and concludes that, when a species occurs in two or more zones, its normal habitat is only in one of them. Thus, *Ascophyllum nodosum*, an Upper Boreal species, in the southern portion of its range fruits only in winter ((148) p. 395; cf. also (10) p. 829). The southern limit of *Fucus virsoides* in the Adriatic is determined by temperature (140), while Isaac (160) p. 145) emphasises the importance of this factor in South African waters.

The effect of temperature is, however, not easily separated from that of illumination which, variable both in duration and intensity in different latitudes, probably also plays a rôle in determining the quality of their algal vegetation; one can, however, scarcely admit Tilden's (169) theories, which are quite unsupported by fact. Temperature, owing to its influence on the rate of respiration, will affect the capacity of a sublittoral alga to thrive below a certain depth. Lami (88) draws attention to the possible importance of mists and prevalent cloud in relation to the distribution of Algae. The effects of diminished salinity have already been considered (p. 6).

Zones of algal distribution do not necessarily correspond to degrees of latitude, since ocean currents traversing the coasts often influence the temperature of the water and cause apparent anomalies in distribution. Reference need only be made to the marked differences at equivalent latitudes between the algal flora on the eastern shores of North America and the western shores of Europe ((14) p. xv; cf. also (24) p. 7) due to the influence of the Gulf Stream, and to the pronounced contrast between the seaweed vegetation on the eastern and western shores of the Cape Peninsula, due to the Antarctic current skirting the western shores. The flora of the latter comprises *Laminaria pallida*, *Ecklonia* and *Macrocystis pyrifera* (see map 2, p. 252), which are practically wanting on the opposite coast ((28), (60) p. 123, (61) p. 20, (92), (185)).

Boergesen's and Jónsson's (14) analysis of the distribution of seaweeds in northern latitudes, with special reference to the flora of the Faeroes, also essentially recognises the temperature-factor. They classify the northern seaweeds in five groups, viz. (*a*) an arctic element (not represented in the Faeroes); (*b*) a subarctic element with species represented in the Arctic Sea and in part extending southwards to England (*Chaetopteris plumosa*, *Agarum cribrosum*, *Alaria Pylaii*, *Phyllophora Brodiaei*, *Halosaccion ramentaceum*, etc.); (*c*) a boreal-arctic element extending from the Arctic as far south as the Atlantic coast of North Africa (*Ascophyllum nodosum*, *Bangia fusco-purpurea*, *Ahnfeltia plicata*, etc.); (*d*) a cold-boreal element, extending northwards to Iceland, the Faeroes and North Norway and southwards to the Mediterranean and North Africa (*Elachista scutulata*, *Castagnea virescens*, *Alaria esculenta*, *Laminaria saccharina*, *L. Cloustoni*, *Gigartina stellata*, *Cystoclonium purpureum*, *Furcellaria fastigiata*,

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etc.); and (*e*) a warm-boreal element (*Leathesia difformis*, *Cutleria multifida*, *Halidrys siliquosa*, *Arthrocladia villosa*, *Sporochnus pedunculatus*, *Taonia atomaria*, *Chondrus crispus*, *Plocamium coccineum*, *Laurencia pinnatifida*, *Callithamnion corymbosum*, *Rhodophyllis bifida*, *Gracilaria confervoides*, *Sphaerococcus coronopifolius* (see map 1), etc.). This grouping has been adopted by many subsequent workers ((24), (49), (80) p. 250, (131) p. 20, (166)). The marine flora of Holland, though poor in species, is essentially like that of the adjacent coasts of Britain and France ((49) p. 170).

On the Atlantic coast of North America, Harvey ((54) p. 25) first pointed out that the Cape Cod Peninsula sharply segregates the northern from the southern seaweeds, and this corresponds to the isothere of 20° C. ((147) p. 201, (150)). The northern area, which probably extends to Greenland, includes many species found on the Scandinavian coast, while the larger *Fuci* and other Brown Algae occur only in colder spots south of the peninsula (cf. also (27), (36) p. 4, (166) p. 2, and map 2, p. 252). A similar dividing line is recognisable on the coasts of Spain and in the region of the southern Japanese sea. Gail (43), on this basis, distinguishes the entire seaweed population of the Northern Hemisphere into a northerly *Laminaria* region (with Ectocarpales, Bangiales and Gigartinales) and a southerly *Sargassum* region (with Siphonales, Dictyotales, and Ceramiales). On the coast of North Carolina ((56) p. 391) the transition between northern and southern floras is indicated by the simultaneous presence of *Fucus vesiculosus* and of numerous Florideae with a marked southerly range. According to Collins and Hervey ((22) p. 8) the flora of Bermuda has much in common with that of Florida and the West Indies (cf. also (178), p. 490).

The Pacific shores of North America afford an analogous picture, although the cold current that skirts a considerable part of the coast results in a pronounced southerly displacement of the Laminariales. Point Conception approximately marks the limit between the northern and southern vegetation ((132) p. 393), although Gail (43) would put it at Cape Blanco. The southern shores of the Japanese islands harbour a considerable number of seaweeds belonging to the Indo-Pacific region ((109) p. 960, (191)), which extend southwards to Australia and westwards to the Red Sea (p. 12), while comparatively few of these appear to occur on the American Pacific shores, where the similarities with the Japanese flora refer more to the subarctic element comprising several striking members of Laminariales (p. 254). Okamura (111) has made a detailed analysis of the distribution of marine Algae in Pacific waters.

Only brief reference can be made to other regions of the world. The tropical seaweed flora is distinguished especially by the abundance and variety of Siphonales and the dominance of Florideae (especially Ceramiales); the most important of the Phaeophyceae are

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Dictyotales and species of *Sargassum* and *Turbinaria*, while Laminariales are completely lacking. It would seem that the algal flora of the Tropics shows a greater measure of resemblance to that of the Southern than to that of the Northern Hemisphere. A considerable number of seaweeds (*inter alia* diverse Sporochnales and Sphacelariales, many Rhodomelaceae and Delesseriaceae) are restricted to the Southern Hemisphere (cf. (53)). The marine flora of New Zealand has something in common with that of Australia, but also includes an evident Antarctic element, some of the representatives of which are also found in South Africa ((87); cf. map 2, p. 252); there are a considerable number of endemic species. *Carpophyllum* occurs throughout New Zealand, while *Durvillea* (associated with *Macrocystis* and *Marginariella*) is dominant in the south ((112) p. 518). The flora of the Chatham Islands shows a general resemblance to that of New Zealand (126).

The Subantarctic and Antarctic floras ((25) p. 152, (44) p. 105, (86) p. 77, (157) p. 156, (179)) include several species with a circumpolar distribution, as examples of which *Scytothamnus australis*, *Halopteris funicularis*, *Durvillea antarctica*, *Macrocystis pyrifera*, *Iridaea cordata*, *Ballia callitricha* (see map 1, p. 8), and *Gigartina radula* may be mentioned. In Antarctic seas species of *Desmarestia* play a very prominent part in the sublittoral region, accompanied by *Lessonia* and *Scytothalia*, while *Durvillea* and *Macrocystis* are more particularly characteristic of the Subantarctic zone ((126*a*) p. 182, (179) p. 65).

There is often an appreciable degree of correspondence between the flora of coasts separated by thousands of miles of ocean or by intervening land-barriers. These similarities can in general only be explained by taking into consideration the changes that have affected the distribution of oceans and of land-masses within recent geological epochs. During the Tertiary period, when there was a land-connection between Europe and America by way of the Faeroes and Iceland, the arctic flora to the north of it probably differed from that to the south ((10) p. 806, (125) p. 98); when the connection was broken, a mingling of the two floras ensued. During the glacial epochs this vegetation was forced southwards into the Atlantic and Pacific Oceans and a flora, which was arctic in character, probably occurred as far south as England and Northern France. With the advent of a warmer era many of the arctic species were again driven northwards, while others capable of adapting themselves to a wider range of temperature remained to form the present-day element common to the North Pacific and Atlantic Oceans. Kjellman ((71) p. 56) established that nearly 60% of these species also occur in the Arctic Ocean.

There are, however, many seaweeds common to the Atlantic and Pacific which are lacking in the Arctic (e.g. *Chorda filum*, *Fucus vesiculosus*, *Saccorhiza dermatodea*), and these are probably more southern types which migrated northwards during the warmer post-

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glacial epochs ((154) p. 184), at a time when the habitat was still continuous. Simmons ((154) p. 176) regards the greater measure of similarity between the seaweed flora of the Polar Sea and the North Atlantic, as contrasted with the North Pacific, as due to the existence of greater opportunities for migration afforded by the more numerous coastal paths. In the White Sea ((47a) p. 20) the Atlantic element has only penetrated into the northern part.

Rosenvinge ((131) p. 40) concludes that the algal flora of the Danish seas migrated into it from the North Sea after the glacial epoch, while Levring ((91) p. 163) regards that of the Baltic as a remnant of the North Atlantic flora which became established during the *Littorina*-period. There is also a considerable subarctic element ((125) p. 95, (161) p. 52).

It has long been assumed that certain genera of sea-grasses (*Posidonia*, *Cymadocea*), which are found both in the Mediterranean and in the Indian Ocean, owe their present distribution to migration from the latter into the former during Tertiary times when there was an open connection between the two. A similar relation is probable for *Acanthophora Delilei* ((37) p. 289; see map 1), for the species of *Vidalia*, for those of the *Bursae* section of the genus *Codium* ((163) p. 55), and for several other genera. Apart from this Indo-Pacific element, the Mediterranean flora also includes a number of genera and certain species (e.g. *Halimeda Tuna*, *Hydroclathrus cancellatus*, *Hypnea musciformis*, *Digenea simplex*, *Taenioma perpusillum*) that are widespread in all warmer seas, but the bulk of the flora ((37) p. 291) is composed of an element that has arrived from the Atlantic. Part of this consists of species common to the Mediterranean and the tropical and subtropical Atlantic (e.g. *Caulerpa prolifera* (see map 1), *Acetabularia mediterranea*, *Nereia filiformis*, *Gracilaria armata*), while another part comprises species widely distributed in the North Atlantic, many of which reach the southern limit of their distribution in the Mediterranean (e.g. *Stilophora rhizodes*, *Taonia atomaria*, *Sphaerococcus coronopifolius* (see map 1), *Chondria dasyphylla*); this second group probably includes many species which were forced southwards during the glacial epochs (cf. also (176)). The Guernsey flora includes a number of Mediterranean species ((96) p. 45).

Many species and varieties found in the Mediterranean are closely related to forms found in the adjacent Atlantic, a fact which has been specially emphasised by Sauvageau ((134), (136) p. 3, (138) p. 17) in relation to the species of *Cystoseira* (cf. also (26)). He points out that those inhabiting the eastern Mediterranean differ markedly from the oceanic species, although the latter show much agreement with the *Cystoseiras* of the western Mediterranean. Feldmann ((37) p. 297) also instances the Mediterranean *Phyllophora nervosa* (DC) Grev., which is closely related to the North Atlantic *P. epiphylla*. The marine flora of the Azores ((142) p. 108) includes many species common to the

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Mediterranean and North-west Europe, but there is also a tropical element. That of the Red Sea has been analysed by Nasr (187).

Boergesen ((11) p. 492) has shown that several seaweeds of the Indian and Pacific Oceans (e.g. *Anadyomene stellata*, *Dictyosphaeria favulosa* (see map 1), *Neomeris annulata* and other Siphonales, *Liagora valida* Harv.[1]) also occur in the West Indies, though lacking at the southern extremities of Africa and America. Murray ((105) p. 172, (106)), who first drew attention to this fact, explained the discontinuity by assuming a warmer climate at the Cape in earlier epochs. During the Pliocene and Oligocene, however, the Caribbean Sea was connected to the Pacific Ocean, the isthmus of Panama being of comparatively recent date, and Svedelius ((163) p. 9) ascribes the above-mentioned similarities to this interoceanic connection. This view is based primarily on the present-day distribution of the tropical sea-grasses ((153) p. 572) and of the species of *Caulerpa*, but stress is also laid (p. 29) on the occurrence of pairs of closely related (vicarious) species of diverse genera (*Udotea* (see map 1), *Padina*, *Scinaia*, *Galaxaura*, *Martensia*, etc.) in the Indo-Pacific region and the West Indies respectively. The present distribution indicates that the Indo-Pacific Ocean was the centre from which most of the new types migrated into the Atlantic, although the species of *Dasycladus*, for example, are assumed to have originated in the Atlantic. Since species showing a discontinuous distribution must have existed prior to the severance of the sea-connection between the two oceans, the bulk of tropical Phaeophyceae and many of the Rhodophyceae must be of younger date than the marine Chlorophyceae.

Many species ((12) p. 4), which are common to the West Indies and to the Canaries, seem to reach the eastern limit of their distribution on the shores of the latter or possibly on the adjacent coast of Africa, which is yet scarcely explored. Half the species recorded for the Canaries, moreover, also occur on the Atlantic coasts of America, and the existence of this common element lends some support to the theory of a former land-connection between America and Africa. Taylor (165) concludes that the marine flora of Brazil presents much similarity to that of the West Indies.

Many striking instances of discontinuous distribution, for which there is at present no satisfactory explanation, are afforded by the presence of species, found at the Cape and in West and South Australia, also to the north of the Tropic of Cancer (Japan, Arabian Sea ((13) p. 58; cf. also (153) p. 574)), although they are apparently lacking in the intervening tropical zone. This is paralleled by the occurrence, both in the Arctic and Antarctic, of a number of species which are not known to occur in the equatorial belt ((44) p. 149, (107)), although no species of Laminariales or Fucales is common to the two

[1] This applies also to certain elements of the fauna. See also Setchell's (152) instructive analysis of the marine flora of Tahiti.

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poles. The marked contrast between the algal flora of the Japan sea and that of the Pacific coast-line of Japan is taken by Okamura (110) to indicate the comparatively late origin of the former which until that time is supposed to have formed, together with the Japanese Islands, part of the continent of Asia.

Our knowledge of the geographical distribution of marine Algae is still too limited to provide much positive evidence as to the existence of endemic genera and species. Attention may, however, be drawn to the numerous Florideae (especially Rhodomelaceae) at present only known from the Australasian region and to the genus *Coccophora* apparently confined to the Japan sea ((110) p. 591). Feldmann ((37) p. 297) recognises *Laminaria Rodriguezii* (p. 196) and *Rissoella verruculosa* as endemic species in the Mediterranean, the latter characteristic of wave-swept rocks in the littoral region ((112*a*) p. 84).

Certain marine Algae have doubtless been introduced into new geographical areas, probably for the most part conveyed on ships' bottoms. Comparatively recent arrivals in Europe are *Colpomenia* (p. 109) and the species of *Asparagopsis* (p. 480), which have been brought from Australia and Japan (cf. also (38), (57), (173)). After storms considerable masses of seaweeds are often cast up on the shore ((21), (40) p. 174, (129), (188)), many of them bearing viable reproductive organs. It is known, moreover, that many Florideae in particular can regenerate from quite small fragments of their thalli (114, 170, 171). Ocean currents will likewise serve to distribute detached portions of seaweeds, while birds may play a part ((10) p. 809, (189)). The fact that seaweeds become established on volcanic and newly arising coral islands indicates that agencies such as those mentioned must be effective. It remains doubtful, however, whether any very considerable number of marine Algae possess the capacity to become naturalised on shores to which they are transported by these means ((87) p. 305, (133), (136) p. 3, (163) p. 18), and it would appear that the spread of most seaweeds takes place rather along coastal stretches than over intervening areas of sea ((125) p. 100).

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Class IX. PHAEOPHYCEAE

While the Algae considered in the first volume comprise in the main freshwater and terrestrial forms, the Phaeophyceae or Brown Algae are practically restricted to the sea. The few freshwater genera (*Pleurocladia*, *Heribaudiella*, *Bodanella*) all belong to the Ectocarpales, while true terrestrial types are unknown. Many Phaeophyceae of the littoral zone are, however, highly equipped to resist exposure during intertidal periods, and a number of Fucales have become adapted to life under the special conditions obtaining on salt-marshes (p. 383).

Although certain genera are largely or entirely restricted to the warmer seas (e.g. *Hydroclathrus*, *Chnoospora*, most Dictyotales, *Sargassum*, *Turbinaria*), the Brown Algae attain their maximum development, both as regards numbers of species and of individuals, in the colder waters of the Northern and Southern Hemispheres. Batters ((5) p. 22) and Newton (173*a*) both enumerate 74 British genera, while Taylor (237*a*) has 57. Many distinctive forms occur in the Pacific (218). Certain orders (Sporochnales, Sphacelariales) and genera (*Splachnidium*, *Ecklonia*, *Lessonia*, many Fucales) are better represented or exclusively found in the Southern Hemisphere.

The abundant and luxurious growth of Phaeophyceae in Subarctic and Arctic regions has been vividly described by Kjellman (101-103); development continues during the darkness of the Arctic winter and many forms produce their reproductive organs at this time at temperatures often below the freezing point ((102) p. 82). Similar data have been provided by Skottsberg ((224) p. 154) for the Antarctic. These facts have been frequently interpreted as indicating that the Brown Algae of the colder seas are shade-forms attaining an adequate excess of photosynthesis over respiration in weak light and at low temperatures ((78) p. 281, (105)). Recent investigations (52, 159) have, however, shown that certain Phaeophyceae, like certain Rhodophyceae (p. 407), have the physiological characteristics of sun-forms, while some can adjust their metabolic processes to the varying light-intensities and temperatures of different seasons ((136), (160), (161) p. 673, (228) p. 53), the larger fucoids being capable of producing as much substance or even more in summer than in winter. Nevertheless, the low rate of respiration at low temperatures and the capacity to photosynthesise in feeble illumination are no doubt important factors conditioning the success of Brown Algae in Arctic and Antarctic regions (cf. also (52) p. 240, (110)).

A large proportion of the Phaeophyceae are lithophytes, so that they are specially prevalent on rocky shores. Many of the forms with large and bulky thalli are surf-loving or, if growing below low-tide level, favour situations where there is a marked current and they are subject

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to the swirl of the waves. No very large number of Brown Algae normally live in deep water, although a few can penetrate to very considerable depths ((11), (203) p. 177, (210) p. 482). The majority inhabit the belt between tide-levels or grow at such a depth that their photosynthetic tissues are displayed but a little way beneath the water-surface.

The Phaeophyceae are in general at a higher level of morphological and anatomical differentiation than the classes previously considered. No unicellular or colonial forms are at present certainly known,[1] nor is the unbranched filament represented. In other words all the simple types of plant-body, so widely found in classes like Chlorophyceae and Chrysophyceae, are lacking. The vegetative body in the least specialised members of Phaeophyceae is a heterotrichous filament, a level of differentiation which is the highest attained among Chlorophyceae.

It is nevertheless highly probable that the evolution of Phaeophyceae has followed the same lines as that of Chlorophyceae, etc., but that the simpler types have either become extinct or still await discovery; there is no apparent reason why they should have perished. The few fossil forms (see p. 42) do not help to elucidate the evolution of the class. The considerable uniformity in pigmentation of the chromatophores, the characteristic fucosan-vesicles (p. 31) implying a specialised metabolism, and above all the constant characteristics of the motile stages (zoospores, gametes, spermatozoids), indicate not only a monophyletic origin, but probably also a derivation from a unicellular flagellate ancestry with motile individuals showing these special features. Pascher (181) at one time believed he had traced a relationship between this hypothetical prototype and the Nephroselmidaceae among Cryptophyceae (1, p. 657), but rightly abandoned ((182) p. 153) this view as further details came to light. The Phaeophyceae are also distinguished by the prevailing isomorphic or heteromorphic alternation in their life-cycle.

The General Features of Vegetative Construction

The heterotrichous filamentous habit exhibited by the Ectocarpaceae (figs. 4 E; 5 J), seemingly the most primitive members of Phaeophyceae, shows a marked degree of parallel with that found in Chaetophorales among Chlorophyceae (62). As there, the Ectocarpaceae include an assemblage of reduced types (p. 58) in which essentially only the prostrate system is present. The parallel may not, however, be pressed too far. The heterotrichous habit thus displayed

[1] There are, however, diverse indications of the existence of palmelloid types possessing Phaeophycean swarmers; cf. the *Pulvinaria algicola* of Reinhardt ((190) p. 127) and the *Phaeocystis Giraudii* (Derb. et Sol.) Lagerh. described by Nasr ((170) p. 3), which has little in common with *P. globosa*.

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in the simplest members of the class is recognisable, at least in early stages of development of the sporophyte, in practically all Ectocarpales (cf. (229) p. 397) and Sphacelariales, although it has disappeared in most of the more specialised orders (Sporochnales, Desmarestiales, Laminariales, Dictyotales, and Fucales); in the Cutleriales it is preserved in a modified form ((257) and p. 169). The persistence of heterotrichy among many of the less specialised Phaeophyceae and its disappearance (i.e. elimination of the prostrate system) in the more advanced forms is altogether paralleled among Florideae (p. 445). In those Brown Algae, which exhibit heteromorphic alternation, the gametophyte (except in *Cutleria*) always shows traces of the heterotrichous habit.

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The bulk of the seaweeds belonging to Phaeophyceae are compact multicellular types with a more or less evident differentiation of tissues. This is specially marked among Laminariales and Fucales, where it is combined with a marked degree of external differentiation and, in some members of the former, with dimensions that vie with those of the larger land-plants. The elaborated sporophytes of Ectocarpales are produced in one of two ways, viz. either (*a*) from a single uniseriate filament or from aggregates of such filaments by dense juxtaposition of their numerous branches (uni- and multiaxial construction) giving a pseudo-parenchymatous structure, or (*b*) by division in diverse planes of the cells of a primary filament giving a true parenchymatous structure. The filaments by the elaboration of which the mature body is thus produced belong to the erect system of the primary heterotrichous stage. The details are given under the individual forms, and it must suffice to indicate here that in *Leathesia* (fig. 17) and *Castagnea* (fig. 21 E), for instance, the construction is multiaxial (cf. *Codium* among Siphonales), in *Spermatochnus* (fig. 27) uniaxial (cf. *Dasycladus* among Siphonales), whilst parenchymatous members of Ectocarpales are exemplified by such types as *Punctaria* (figs. 31, 32 C), *Scytosiphon* (fig. 34), and *Asperococcus* (fig. 37). In uniaxial and parenchymatous types several erect-growing sporophytes commonly originate from the same prostrate base (fig. 31 A), and this is no doubt sometimes also true of multiaxial forms. While special types of uni- or multiaxial thalli are met with in Desmarestiales, Sporochnales and Cutleriales, most Phaeophyceae are true parenchymatous forms and in this respect contrast markedly with the Red Algae.

The structures produced in the diverse ways indicated above undergo strengthening and elaboration by two methods which are probably interrelated, since in both there is an outgrowth from already mature cells of threads which are commonly branched. In many uniaxial (*Spermatochnus*, fig. 27 B, F; *d*; *Desmarestia*, fig. 61 A, *e*) and parenchymatous (e.g. Sphacelariales, fig. 94) types such filamentous outgrowths arise superficially and, growing intimately apposed to the surface and to one another, become compacted to form

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an enveloping cortex which may increase in thickness by cell-division. Such superficial threads usually contain chromatophores and are most suitably designated *cortical threads*. Quite similar structures often arise in the basal parts of the thallus and, spreading over the primary attachment system, fulfil a subsidiary rôle in anchorage, so that in these instances they could with equal justification be called *rhizoids*. In many Brown Algae (*Chordaria*, fig. 22 D, *hy*; Laminariales, fig. 83 B, *hy*; Fucales), however, the outgrowing threads originate from internal cells and ramify in diverse directions through the tissues. Such structures are usually devoid of chromatophores and may be called *hyphae*. For the most part they probably fulfil conducting and mechanical functions and in relation to the latter are commonly thick-walled. There is no sharp distinction between cortical threads, hyphae, and rhizoids, all of which are merely diverse expressions of the capacity of the algal cell to form thread-like outgrowths. The latter commonly originate from the lower ends of the parent-cells, affording evidence of polarity.

In many parenchymatous types, after the primary longitudinal septation demarcating a peripheral from a central series of cells, further cell-division tends to be restricted to the superficial layer (figs. 33 C; 35 E). The cells of this meristem divide periclinally, the segments cut off internally being added to the central tissue, while occasional anticlinal division in the surface-layer enables it to keep pace with the increasing girth of the whole. This superficial meristematic activity, which is little marked among the parenchymatous Ectocarpales, becomes a pronounced feature in Laminariales (fig. 83 C) and Fucales (fig. 130 B), where it is responsible for the marked increase in thickness attained by the older parts. It is also met with in some of the pseudo-parenchymatous forms.

The often abundant branching of the laterals borne on the axial threads of the pseudo-parenchymatous forms, which leads to the formation of a compact cortical region, and the superficial growth of parenchymatous forms just discussed, often result in marked tensions between the external and internal tissues. Such *tissue-tensions* (cf. (90) p. 25, (97), (116) p. 828, (168) p. 13, (246) p. 13) are due to a state of compression in the outermost tissues, while the internal elements are more or less markedly stretched. As a consequence longitudinal strips of the thalli of *Dictyosiphon*, *Chordaria*, *Desmarestia*, *Chorda*, etc., especially when placed in water, curve with the outer tissues on the convex side; not uncommonly such strips roll up into a complete circle. Similar tensions are realised in the stipes of Laminariales and in all instances they probably contribute to the flexibility of the structures involved. The extensibility of such thalli varies (50), being slight in *Fucus*, which has considerable tensile strength, and more considerable in *Halidrys*, *Ascophyllum*, and *Laminaria* (cf. also (245) p. 9). The massive tissues formed by many Brown Algae are for

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the most part completely devoid of intercellular spaces, although certain forms develop numerous air-bladders.

The Phaeophyceae afford some of the best examples of intercalary growth among lower plants. The intercalary meristems are typically located at the base of a hair, to the increase in length of which they contribute to some extent, although the bulk of the segments are cut off below the meristem (figs. 5 D; 24 A). This *trichothallic growth* is found in many Ectocarpales, Desmarestiales, Tilopteridales, and Cutleriales. Intercalary growth is also met with in Laminariales, where the seat of the meristem is the transition zone between stipe and blade. Such well-defined intercalary meristems are not, however, represented in all Ectocarpales, and in many Ectocarpaceae the growth is diffuse.

Intercalary growth has, moreover, been replaced by apical growth in a number of evolutionary lines among Ectocarpales, as well as in Sphacelariales, Dictyotales, and Fucales. There is considerable evidence to show that, in certain Ectocarpales (pp. 90, 112) and Fucales (p. 349), the apical cell of the mature plant is at first differentiated beneath a hair with a basal meristem. Although no such sequence is observable in other series with apical growth, the instances cited and the prevalence of intercalary growth among the less specialised members suggest that apical growth in this class is a secondary acquisition (cf. also (135) p. 59).

The Phaeophyceae exhibit not only marked internal differentiation, but also display a great range in external form, especially in the more advanced orders. This is fully illustrated in the subsequent detailed consideration. In many Ectocarpales the thallus consists of branched cylindrical or flattened strands presenting little outward differentiation, but the Punctariaceae exhibit a surface-development presenting many analogies with that of the Ulvaceae among Green and of the Bangiales among Red Algae; the thallus in Punctariaceae is, however, based on a heterotrichous system (p. 100). Marked morphological elaboration, accompanied by the development of pseudo-axillary branch-formation, is met with in some Sphacelariales (p. 274). A foliose differentiation of certain parts of the thallus is specially characteristic of Laminariales and Fucales, the leafy expanses of which are either differentiated parts of the thallus (*Laminaria*) or represent special outgrowths (Alariaceae, *Sargassum*) (cf. the gametophytes of Hepaticae). At the same time the Laminariales exhibit a method of thallus-elaboration by progressive splitting of the primary foliar expanses that is unique among Thallophyta. Dichotomous branching is typical of many Dictyotales and some Fucales, the latter showing a striking developmental series in which monopodial progressively replaces dichotomous branching.

Although many Brown Algae (*Ralfsia*, *Lithoderma*, many Laminariales and Fucales) are lithophytes, a considerable number (Ectocarpales, Sphacelariales, etc.) are epiphytes. In diverse of these some

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of the filaments (figs. 7 D, E; 16 B, E) penetrate into the foreign tissue to an appreciable depth and the non-endophytic part of such forms is commonly reduced to a more or less marked extent. As a general rule the endophytic filaments possess chromatophores and only traverse the gelatinous walls of the host, although diverse instances are on record of actual penetration of the cell-cavities (p. 58). It is scarcely possible to speak of parasitism since, although the contents of the host's cells adjacent to the endophytic filaments are commonly disorganised or destroyed (cf. e.g. (202) p. 230), there is no evidence that the endophyte draws any nourishment from them. The fact that fucosan is usually lacking in the vicinity of the endophytic filaments (cf. e.g. (28) p. 9) is proof of some change, but not of parasitism. True parasites, destitute of photosynthetic pigments, are lacking.[1]

The Cell-wall

The cell-walls of Phaeophyceae are commonly gelatinous and appear to consist of pectic substances with a layer giving the reactions of cellulose adjacent to the protoplast;[2] according to Kylin ((121) p. 346) calcium is present in the middle lamella. Diverse gum-like mucilages have been extracted with water, the chief being algin (226) and fucoidin ((120) p. 191, (121) p. 404). The latter, especially abundant in *Laminaria* (cf. also (64) p. 36), though found also in *Fucus* and in very small quantities in *Ascophyllum*, is, according to Bird and Haas (10), a carbohydrate ester of sulphuric acid (cf. also (73), (260)). Algin seems to be more widely distributed ((29), (86) p. 47, (87), (99), (141), (262)); that of Laminariales is stated to be a polymer of mannuronic acid (10, 173). It has many economic uses, being employed in the preparation of adhesives, artificial silk, etc. (265). A third substance, fucin ((87), (121) p. 412, (251) p. 635) is, according to Miwa (154), very similar to algin and likewise contains sulphur (155). Magnin ((142) p. 646) states that callose is present in the cell-membrane in *Ascophyllum nodosum* and *Laminaria digitata*. Callus is widely distributed in the sieve-tubes of Laminariales.

The abundant mucilage of the larger Brown Algae is only in certain Laminariales located in definite mucilage-canals (p. 238). It can hardly be doubted that it plays a significant rôle in the survival of the littoral Fucales during exposure. Pringsheim ((188) p. 252; cf. also

[1] Fungal parasites do not appear to attack Brown Algae very frequently. *Dothidella Laminariae* Rostr. occurs on diverse species of *Laminaria* ((56) p. 10, (98) p. 149) and Estee (55) reports galls due to *Guignardia* on *Cystoseira* and *Halidrys*. Ollivier (178) records Chytridineae on *Ectocarpus* (cf. also (267)) and a Pyrenomycete (*Melanopsamma*) on various Brown Algae (see also (178*a*) p. 165), while Schiffner ((209) p. 172) found an *Olpidium* on the propagules of *Sphacelaria tribuloides*. According to Brandt ((14) p. 32) *Macrocystis* and other Laminariales are subject to a bacterial disease.

[2] See (80) p. 122, (99), (121) p. 347, (154), (168) p. 10, (172), (180), (201) p. 181, (224) p. 121, (240) p. 39, (246) p. 47.

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(84) p. 78) concludes that the water-holding capacity of *Fucus* is due to the cell-membranes and not to the osmotic properties of the cells.

Calcification of the membrane is very exceptional, although met with in species of *Padina*, where the incrustation consists of arragonite (187). Iron incrustation is likewise uncommon; it is recorded especially in *Padina* ((156) p. 12) and Sphacelariales ((223) p. 113).

The Protoplast

The cytoplasm of Phaeophyceae does not exhibit the marked viscosity seen in many Red Algae. Plasmolysis is easily effected ((133) p. 241) and, although complete rounding off of the protoplast is rarely obtained, there is no marked adhesion to the cell-walls ((93) p. 393). The capacity for deplasmolysis varies ((9), (15) p. 446, (88) p. (55)). The mitochondria, appearing as rounded (fig. 1 P, *ch*) or filiform bodies, have been studied especially by the French school ((24) p. 161, (41), (91), (145), p. 112). They are not affected by *intra vitam* stains that colour the vacuolar contents, but as a general rule are stained by iron haematoxylin after fixation (10% formalin in sea-water). An origin of the chromatophores from mitochondria has been advocated ((67) p. 285, (174)).

The cells commonly possess numerous small vacuoles (fig. 1 H, K, L, *v*) separated by delicate cytoplasmic lamellae ((31) p. 452, (34) p. 421, (145) p. 110, (244)); in Sphacelariales (fig. 91 G), in particular, the numerous vacuoles give an alveolar structure to the cytoplasm ((255) p. 118; see also (167) p. 166). A single central vacuole is, however, reported in *Dictyota*, species of *Fucus*, *Sporochnus*, etc. According to Chadefaud ((18), (24) p. 184) the sap includes colloidal substances (metachromatin), very abundant in *Desmarestia* ((131) p. 6), which are responsible for the *intra vitam* staining with neutral red or cresyl blue and are sometimes slowly precipitated by the latter as granules or crystalline clusters (fig. 1 K, *m*; P, *e*); some of these may be due to iodides ((126) p. 56, (149)).

The reaction of the vacuolar contents is neutral or alkaline ((4) p. 786, (18), (24) p. 184; (131) p. 5, (145) p. 139); Kylin ((121) p. 348) found it to be neutral or very slightly acid in Laminariales and Fucales. Aqueous extracts, on the other hand, are acid (27), with a *p*H of 4·6–6·8 ((130) p. 646). In diverse species of *Desmarestia* the extract is stated to have a *p*H of about 1 (250), although there is difference of opinion as to the nature of the acid present (128), (250). The bluish colour assumed by certain species of this genus (e.g. *D. viridis*) after death is due to the action of the acid sap on the fucoxanthin of the chromatophores. The osmotic pressure, determined cryoscopically, lies between 30·2 and 31·8 atmospheres in diverse Fucales ((165) p. 131), while Hurd (95) by a less precise method determined it as 22·7 atmospheres in *Nereocystis*. Kylin ((133) p. 241) gives much higher values and points out that the

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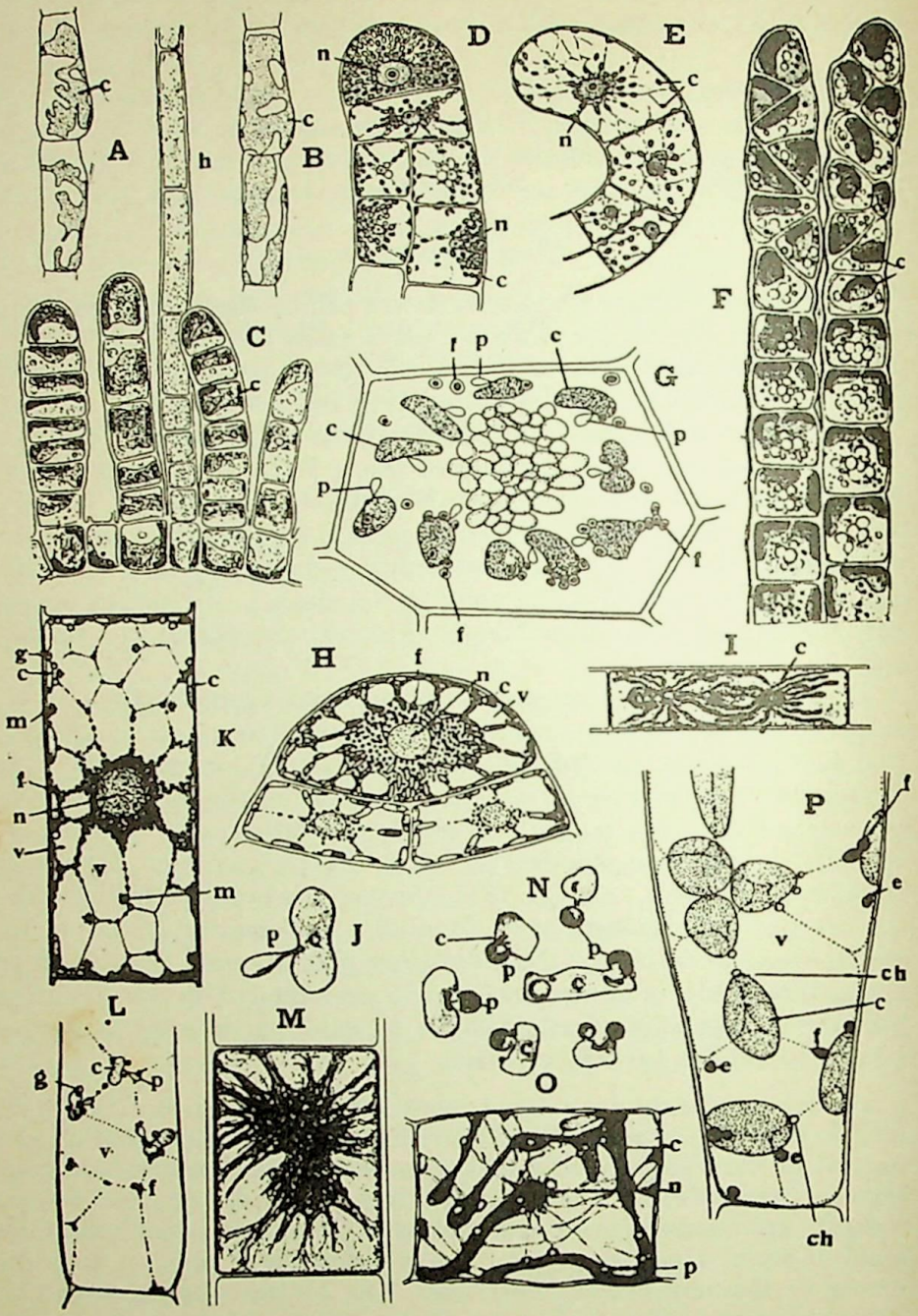

Fig. 1. Chromatophores of Phaeophyceae. A, B, *Carpomitra costata* (Stackh.) Batt., cells of gametophyte. C, *Ascocyclus secundus* Strömf., vertical section. D, *Taonia atomaria* J. Ag., apex of thallus in section. E, *Padina pavonia* J. Ag., longitudinal section through apex. F, *Lithoderma fatiscens* Kuck., two erect threads. G, *Asperococcus bullosus* Lamour. H, *Dictyota dichotoma* (Huds.) Lamour., apex. I, M, *Pylaiella fulvescens* (Schousb.) Born. J, L,

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younger cells often have a somewhat higher osmotic pressure than the older ones.

Chromatophores and Pigments

The chromatophores of Phaeophyceae are almost invariably parietal. Axile chromatophores are recorded only in *Pylaiella fulvescens* (fig. 1 I, M), where they are stellate structures something like those of a *Zygnema* and present to the number of one or two in each cell (12). In the vast majority of Brown Algae the photosynthetic cells contain numerous small discoid chromatophores (fig. 1 D, E, K, P, *c*; (24) p. 146, (211) p. 34, (213) p. 11).

Among Ectocarpales there is, however, some variety of form. In diverse genera the cells contain but a single, usually plate-shaped chromatophore (species of *Ectocarpus*; *Ascocyclus*, fig. 1 C; diverse Myrionemataceae; *Petalonia Fascia* (217) p. 111; *Scytosiphon Lomentaria* (193) p. 214; *Colpomenia* (208) p. 329). In others the number of chromatophores is limited. Thus, in *Lithoderma* (fig. 1 F; (114) p. 166) there are 4–8 and in *Hecatonema terminalis* (Kütz.) Kyl. ((193) p. 215) 2–3 curved plate-shaped chromatophores in the cells, often fitting closely together; much the same obtains in *Dictyosiphon*. Ribbon-shaped chromatophores occur in some species of *Ectocarpus* (fig. 1 O; (109) p. 308, (213) p. 14) and in *Phloeospora* ((193) p. 215), where they are branched; in *E. confervoides* the ribbon is often narrow and spirally twisted. In the older cells of these species of *Ectocarpus*, however, one often finds a considerable number of small discs. The occurrence of single chromatophores in diverse Ectocarpales is in conformity with the general low level of differentiation exhibited by this order. It is probably correct to assume that, as in other classes of Algae, this marks the primitive condition and that the occurrence of numerous discoid chromatophores represents a more advanced state. The single dissected chromatophore in the gametophyte of *Carpomitra* (fig. 1 A, B) is in marked contrast to the numerous discoid chromatophores of the sporophyte ((207) p. 155).

The small chromatophores within the apical cells of *Fucus* and *Cladostephus* ((143), (145) p. 133) undergo appreciable enlargement in the outer, although they remain small in the inner cells of the mature thalli; the reproductive organs also contain small plastids. A similar enlargement and flattening of the chromatophores is recorded by

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Mesogloea sp., stained with cresyl blue; J, single chromatophore, with pyrenoid. K, *Pylaiella littoralis* (L.) Kjellm. N, O, *Ectocarpus siliculosus* (Dillw.) Lyngb.; N, chromatophores with pyrenoids. P, *Fucus vesiculosus* L., cell of hair, stained with cresyl blue. *c*, chromatophore; *ch*, mitochondria; *e*, endochromidia; *f*, fucosan-vesicles; *g*, fat-globules; *h*, hair; *m*, semi-crystalline deposits in vacuole; *n*, nucleus; *p*, pyrenoid; *v*, vacuole. (A, B after Sauvageau; C after Reinke; D, E after Senn; F after Kuckuck; G after Kylin; I, M after Boergesen; N, O after Knight; the rest after Chadefaud).

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Senn (217) in diverse Dictyotales. The stigma in the motile elements of Phaeophyceae is, according to Chadefaud ((21), (24) p. 153; cf. also (147)), invariably differentiated as part of a plastid (cf. fig. 43 L, N).

Many Brown Algae show movements of the chromatophores in response to changes in the intensity and direction of illumination ((117), (205), (206) p. 9, (217)). When the light is of medium intensity the chromatophores take up a position against the external walls, while in bright light there is movement to the side walls. Since the fucosan-vesicles remain stationary during such changes, Senn ((217) p. 136) concludes that there is active movement of the plastids themselves. Hypertonic solutions cause the chromatophores of Dictyotales to take up a surface position, whilst in hypotonic solutions they tend to shift to the side walls (117). According to Senn the chromatophores of diverse Phaeophyceae (Dictyotales, *Zanardinia*, *Asperococcus*) assume a spherical or ellipsoidal shape in weak light or darkness, while Sauvageau (205) records contraction of those of *Saccorhiza* in bright light. The single band-shaped chromatophore of *Petalonia* becomes inrolled in weak light. Some Phaeophyceae (*Cystoseira*, *Dictyota*) exhibit a bluish or greenish iridescence in strong light; in *Cystoseira* (cf. (7) p. 699), as in Red Algæ (p. 584), this is due to the aggregation of special protein-masses beneath the external walls (fig. 130 G, *l*).

Bodies of doubtful nature, but since Kuckuck's investigations ((112) pp. 101, 130; cf. also (8) p. 56) usually described as *pyrenoids* (Phaeophycean starch of Schmitz (213) p. 154), occur in diverse Ectocarpales ((119) p. 5, (124) p. 11), as well as in *Haplospora* ((194) p. 114), *Nereia*, and *Arthrocladia* ((8) p. 57); they appear to be lacking in the higher orders. The bodies in question are never embedded in the chromatophores. They are commonly more or less pyriform and attached by their narrower ends to the surface of the latter (fig. 1 G, *p*); in *Mesogloea* (fig. 1 J, L, *p*) they are definitely stalked (cf. *Ochrosphaera*, 1, p. 508). In other instances (e.g. *Asperococcus compressus* (217) p. 109) they appear more or less globose (fig. 1 O, *p*). According to Knight ((109) p. 308; cf. also (25)) the pyrenoids of *Ectocarpus siliculosus* are either closely apposed to the chromatophore or attached to it by a stout or slender strand of cytoplasm (fig. 1 N), the latter condition being regarded as secondary; some evidence is produced for the origin of these bodies from the chromatophores. They are present also during zoospore-formation.

Treatment with a 0·1 % solution of picric acid in seawater causes bursting of the fucosan-vesicles, while leaving the pyrenoids intact ((119) p. 7). Whilst staining like the pyrenoids of other Algae, they do not show the usual protein-reactions ((24) p. 148) and their true character and function still remain obscure. They may represent a metabolic product of a nature different from that of the pyrenoids of other Algae, a view which finds some support in the fact that they can apparently become detached from the chromatophores ((18) p. 157, (213) p. 155; cf. however (119) p. 8).

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The characteristic coloration of Phaeophyceae, varying from olive-yellow to deep brown, is due to an accessory carotenoid pigment, *fucoxanthin* (also called phycoxanthin (153)),[1] which was first isolated by Willstätter and Page ((249) p. 253), although its presence had been recognised long before ((118), (192), (225) p. 461, (242) p. 240). It is accompanied (cf. also (35), (74), (198) p. 214) by chlorophyll *a*, with only small traces of chlorophyll *b*; according to Seybold and Egle ((220) p. 57) the latter is altogether wanting. Howard (02) finds evidence of a chlorophyllase in *Nereocystis*. Various workers report the presence both of carotene (236) and of xanthophyll (fucoxanthophyll of Tswett (92), (125) p. 60, (220) p. 63, (249) p. 249), although Heilbron ((17) pp. 97, 104, (82)) states that β-carotene and fucoxanthin are the only carotenoids present in fresh Fucales and that xanthophylls are lacking; they find evidence, however, of their presence in Ectocarpales and Sphacelariales. Kylin ((134) p. 8) has recently cast doubts on these conclusions. Lubimenko ((139), (140); cf. also (249) p. 252) states that the amount of chlorophyll in Brown Algae is only 30% of that in *Zostera*, whilst Seybold and Egle (220) find that the Brown Algae investigated by them contain just as much chlorophyll and carotenoid pigments per unit of surface as the Chlorophyceae and that the molecular ratio of green and yellow pigments is the same in both. The sublittoral forms are not poorer in pigments than the littoral ones. All Phaeophyceae so far examined contain fucosterol ((17) p. 104, (83)), and flavins are widely represented ((81), (243) p. 260).

An impure solution of fucoxanthin is readily extracted from the dead alga with water, leaving the chromatophores green. The formula is $C_{40}H_{60}O_6$ ($C_{40}H_{56}O_6$ according to Willstätter and Page). The aqueous solution is orange-yellow, whilst the crystals are red-brown with a bluish sheen. There is nothing very distinctive about the absorption spectrum (192), save for the strong absorption of the blue rays (fig. 2 A, *F*). The amount of fucoxanthin varies; *Laminaria*, *Dictyota*, *Petalonia Fascia*, *Pylaiella littoralis*, and species of *Ectocarpus*, for instance, are rich, while the species of *Fucus* are poor in it. According to Montfort ((163) p. 539) the last, like most of the littoral Brown Algae, are rich in xanthophyll and phylloxanthin. Of the two modifications of fucoxanthin previously recognised by Kylin ((125) p. 64) one has proved to be a post-mortem oxidation-product of the other ((82), (134) p. 9).

Until recently it has generally been doubted whether the fucoxanthin participates in any way in the process of photosynthesis. Montfort

[1] The *phycophaein* of earlier writers (153, 214) is a post-mortem oxidation product ((157), (225), (242) p. 236) and, according to Kylin ((118) p. 223, (119) p. 17, (120) p. 172, (124) p. 16), is formed from fucosan. Molisch's view ((157) p. 135, (158) p. 256) that the colour of Brown Algae is due to a modification of chlorophyll called *phaeophyll*, which was stated to give rise to chlorophyll after death, is now only of historical interest.

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((162) p. 761, (163) p. 539; cf. also (164), (212)) has, however, shown that Brown Algae rich in fucoxanthin exhibit a much higher rate of photosynthesis in blue light than those which are poor in it (fig. 2 B); elimination of blue rays effects marked reductions in the photo-

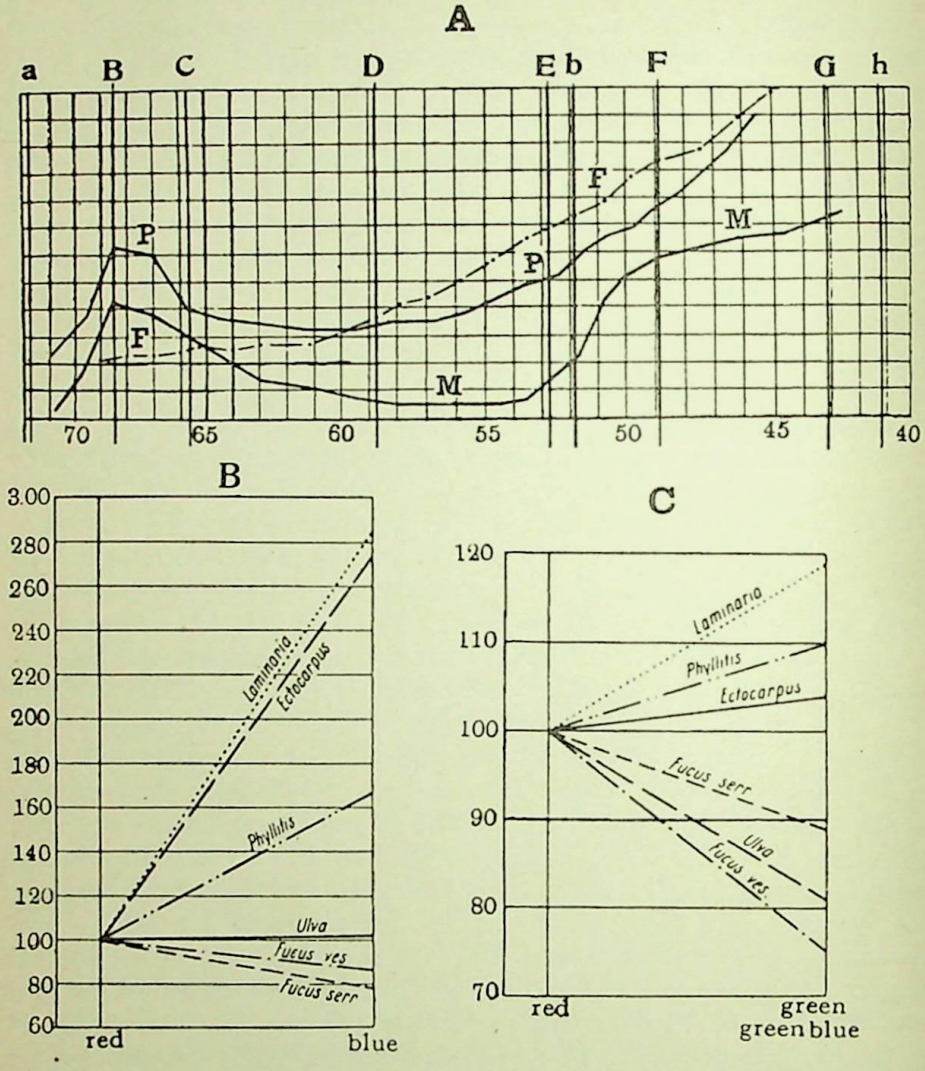

Fig. 2. A, absorption-curves of living *Monostroma* (*M*), living *Petalonia* (*P*), and of a fucoxanthin-solution (*F*, interrupted line) (after Oltmanns). B, relative photosynthesis (apparent assimilation) in red and blue light of diverse marine Algae, in relation to photosynthesis in red light (after Schmidt). C, ditto in red and green light (after Schmidt).

synthesis of such forms. According to Schmidt ((212); cf. also (197)) forms poor in fucoxanthin agree with Green Algae in showing maximum photosynthesis in red (fig. 2 B), a lower maximum in blue, and a pronounced minimum in green light (fig. 2 C), whereas those

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with more fucoxanthin exhibit a maximum in blue, a lesser one in red and a feebly indicated minimum in green light. The two opposing types are not in any way related to the light-intensities in the habitats frequented by the seaweeds in question and are distinguishable both among sun- and shade-forms, although the relative values for photosynthesis in light of long and short rays depends on the intensity of illumination. Both Montfort and Schmidt conclude that fucoxanthin plays a photochemical rôle in photosynthesis. Kniep ((106) p. 122) earlier suggested that the presence of the brown pigment led to a better utilisation of all the incident rays, while according to Shelford and Gail ((221) p. 171) certain sublittoral Laminariales are abundant only down to a depth at which there is still a sufficiency of the shorter wave-lengths. At Puget Sound these seaweeds exhibit a maximum photosynthesis at about 8 metres, whereas *Desmarestia ligulata*, inhabiting deeper water, has the maximum at 15 metres and *Fucus evanescens* at 1 metre (63). Prát (186) shows that many littoral Brown Algae absorb ultra-violet rays.

Fucosan-vesicles

A very characteristic feature of the Phaeophyceae is the presence, especially in meristematic, photosynthetic, and reproductive cells ((20), (24) p. 213, (48), (119) p. 10, (124) p. 12), of large numbers of highly refractive, colourless vesicles which are variously termed *physodes* ((13) p. 166, (24), (30), (33), (34) p. 425, (151) p. 8) or *fucosan-vesicles* ((119) p. 9, (120), (121) p. 402, (124) p. 12, (132)). They were first clearly distinguished from the pyrenoids by Schmitz ((213) p. 155). They are commonly aggregated around the nucleus (fig. 1 H, K, *f*) and vary considerably in size, sometimes reaching a diameter of 4μ or more. The contents are fluid and acid in reaction, so that they assume a reddish violet colour on treatment of fresh material with neutral red, while with cresyl blue (144) they become turquoise blue; the ordinary vacuoles, on the other hand, take on orange-yellow and violet colours respectively with these two reagents in conformity with the alkaline nature of their contents ((18), (24) pp. 184, 216, (131), (132) p. 4, (145) p. 139).

In *Laminaria* Chadefaud (23) records vesicles devoid of fucosan and stained violet with cresyl blue, but Kylin ((132) p. 8) states that these are found only in unhealthy material. Vital staining of the fucosan-vesicles is also readily achieved with methylene blue, while indophenol blue *in statu nascendi* colours them blue-green ((18) p. 159, (24) pp. 190, 217). A very striking reaction, long employed in their demonstration, is the red coloration with vanillin hydrochloride (cf. also (185)). Osmic acid stains them black, which has led to the mistaken view that they contain fat ((13) p. 166, (75) p. 266, (191) p. 328, (240) p. 38).

The contents of the vesicles consist of a substance known as *fucosan* which, although not precipitated by iron chloride ((120) p. 171), shows

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many of the properties of tannins (cf. also (8) p. 56) and is usually regarded as a derivative of phloroglucin ((30) p. 301, (119) p. 18). Hansteen's ((76) p. 346, (77) p. 612) conclusion that the contents were a carbohydrate and represented a first product of photosynthesis is due to confusion with laminarin (p. 33), while his assertion that they are formed by the chromatophores (cf. also (94) p. 72) is due to a failure to distinguish pyrenoids and fucosan-vesicles (32). The latter originate in the cytoplasm, independently of the chromatophores ((132) p. 5, (240) p. 37). Mangenot ((145) p. 141) believed that they arose primarily in the vacuoles, but their occurrence here has been shown to be secondary ((18) p. 163, (19), (48) p. 296) and, according to Dangeard ((42) p. 371), is a pathological condition (cf. however (24) p. 193). The evidence for Chadefaud's view (cf. also (22) p. 45) that fucosan-vesicles develop from mitochondria is inadequate and for the present they may be regarded ((119) p. 9, (124) p. 12, (132) p. 7, (150)) as vacuoles of a special kind, the mode of origin of which is not clear. According to Chadefaud ((24) p. 192) they are formed only in the apical cells in Sphacelariales.

The vesicles not uncommonly show movements which may be accompanied by change of shape ((13) p. 167, (30) p. 296, (77) p. 622, (113) p. 299, (119) p. 10, (124) p. 13) and are sometimes rapid ((48) p. 296); it is not clear whether these movements result from cytoplasmic streaming or from physical causes. There is some evidence that the vesicles can multiply by division ((20), (24) p. 223, (132) p. 8), and Kylin ((121) p. 403) believes that several may fuse. Chadefaud ((24) p. 229) provides data indicating a possible excretion of fucosan.

The structures under discussion occur wherever intensive metabolism is taking place and are no doubt a by-product, which is, however, intimately related to the processes of nutrition[1] ((24) p. 227, (124) p. 18, (132) p. 9, (240) p. 38). Comment is frequently made on the absence of fucosan-vesicles from the cells adjacent to the endophytic filaments of "parasitic" Algae, as for instance in *Ascophyllum* attacked by *Polysiphonia fastigiata* (p. 548); this is evidence of a metabolic disturbance, but does not imply that the vesicles are of the nature of a food-reserve. There does not appear to be any good evidence that they accumulate in the light, in fact in *Ectocarpus siliculosus* an increase during prolonged darkness is recorded ((109) p. 309). Knight reports diminution during nuclear division, while Sauvageau ((206) p. 44) describes a progressive decrease during the maturation of the sporangia of *Saccorhiza*. Fucosan-vesicles are often found in the young cells of hairs (20). In *Fucus serratus* Pontillon (184) observed a greater abundance of the vesicles at low than at high tides, as well as on the side facing upwards during exposure; this latter is not due to

[1] Chadefaud ((24) p. 194; cf. also (151) p. 8) recognises similar structures in certain Xanthophyceae (I, p. 492), as well as in Chrysomonadineae and Euglenineae, but it remains doubtful whether they are of the same nature.

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illumination, since the same effect is observed when the thallus is shaded.

In certain Phaeophyceae (Sphacelariales, p. 265) the fucosan-vesicles accumulate in special cells; such are also the ascocysts of *Ascocyclus* (fig. 8 D, *a*, p. 59) and the "glands" of certain Laminariales ((204), (206) p. 10; fig. 86 D, F, p. 239).

Products of Photosynthesis

Kylin ((120) p. 175, (121) p. 363, (123), (128) p. 10; cf. also (238)) is of the opinion that simple reducing sugars (dextrose) constitute the first products of photosynthesis, but that they occur in such small quantities that they can only be detected after concentration; others ((29), (86) p. 41, (195) p. 421) have failed to obtain evidence of their presence. Haas and Hill (69) found a pentose in the *forma libera* of *Pelvetia canaliculata*, but could not detect it in *Fucus serratus* and *Ascophyllum nodosum*; cf. also the fucose of various investigators ((68), (169) p. 301). Kylin believes he has detected a disaccharide (laminariose).

Of frequent occurrence are dextrin-like polysaccharides grouped as *laminarin*[1] ((120), (121) p. 371, (123) p. 239, (195), (239), (256)). They appear to constitute food-reserves and are believed by Kylin to arise from the simple sugars of photosynthesis. After extraction laminarin appears as a white, tasteless powder soluble in water, the solution being laevorotary. It is not coloured by iodine, assumes a faint red tint with Fehling's solution, and is transformed into dextrose on hydrolysis with sulphuric acid, as well as after treatment with diastase ((121) p. 371). Laminarin is particularly abundant in *Laminaria* (cf. also (64) p. 36), whilst *Fucus vesiculosus* and *Ascophyllum nodosum* contain relatively little; in *Laminaria* it occurs copiously during the summer and is used up in winter ((120) p. 186, (121) p. 398). It appears to be lacking in diverse other Phaeophyceae that have been investigated (e.g. *Halidrys siliquosa*, *Chorda filum*, *Chordaria flagelliformis*, etc.; (29), (123) p. 240). Enzymes capable of hydrolysing carbohydrates have been demonstrated in *Laminaria* (47, 239) and *Nereocystis* (230).

Mannitol appears to be more widely distributed.[2] Haas and Hill ((72) p. 56; cf. also (29)) indeed suggest that it may be universal and that the presence of such sugar alcohols may account for the extreme scarcity of free sugars, which are supposed to undergo immediate conversion into alcohols and polysaccharides. According to Kylin mannitol occurs as a frequent food-reserve in Laminariales, Fucales, etc., but he failed to find it for instance in *Desmarestia viridis* and *Stilophora rhizodes*; in *Laminaria* the amount varies in different seasons ((195) p. 423). The mannitol is sometimes present (70) as an

[1] This is the fucosan of Hansteen ((76) p. 346).

[2] See (64) p. 36, (70), (120) p. 174, (123), (169) p. 299, (195) p. 421, (216) p. 97, (227).

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anhydride (mannitan). Oxalates are recorded in diverse Phaeophyceae ((121) p. 351, (128) p. 10).

Fats are commonly present ((18) p. 156, (20) p. 17, (119) p. 22), being recorded in Fucales (especially *Ascophyllum*), in the young sporangia of *Chorda filum*, in the photosynthetic tissues of *Laminaria*, etc. There is a greater amount of fat ((72) p. 56, (200)) in exposed forms (*Pelvetia*) than in those which are mainly submerged (*Laminaria*); moreover the fats in the former are more highly saturated. There is also some seasonal variation.

The facts indicate that Brown Algae possess a carbohydrate metabolism which shows many distinctive features, although clearly following a course parallel with that of other holophytic plants. Little is known of the nitrogen metabolism. Nitrates are sometimes recognisable in the growing apices (233), although absent from older parts ((121) p. 339, (171) p. 280). In *Laminaria* they are found in the stipe, but there is little in the blade or in the transition zone ((232) p. 83); according to Wille ((247) p. 330) the newly developing blades are richer in nitrogen and phosphorus than the old blades or the stipes. Hoagland ((86) p. 46) concludes that much of the nitrogen present is not in the form of proteins. In the littoral Fucales Haas and Hill ((71), (72) p. 64) found an octapeptide of glutamic acid, although this was lacking in the forms inhabiting the lower zones. It is suggested that this is due to interruption of the normal metabolism of the former owing to the long periods of emersion. In artificial cultures growth is usually markedly increased by the addition of nitrates to the sea-water (122). Phosphates are easily demonstrated in diverse Phaeophyceae ((121) p. 341), while *Desmarestia* is rich in sulphates. The larger Brown Algae have been an important source of potash, to which they largely owe their manurial value.

Diverse Laminariales and Fucales contain considerable quantities of *vitamins* (259, 261, 263), the vitamin C in *Laminaria* being more abundant in spring than in winter.

Iodine

The larger Brown Algae were long one of the sources of commercial iodine (cf. (51), (53)). Whereas sea-water only contains on the average 2 mg. of this element per litre, largely in an organic form (65), the species of *Laminaria* in particular contain appreciable amounts, although the data as to the actual percentage in the dry weight ((6), (57), (64) p. 36, (129) p. 60, (216) p. 96, (247) p. 336) are rather variable. Kylin ((126) p. 59; cf. also (57), (241)) gives the following percentages of KI in the fresh weight: *L. saccharina*, stipe, 0·19; transition zone, 0·30; *L. Cloustoni*, stipe, 0·30; other data for Laminariales are: *Nereocystis* ((196) p. 91), 0·08–0·22%; *Eisenia bicyclis* (177), 0·15–0·35%. On the other hand the amount in Fucales is less, being only 0·02% in

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Himanthalia, although Scruti (215) gives for *Sargassum linifolium* 0·12 % or less (cf. also (237), (268)). Kylin (126) also quotes low values for many other Brown Algae. In *Laminarias* there is more iodine in the younger than in the older parts, and the amount is greatest in July and decreases markedly in autumn (60), (61), (215). Opinions differ as to the form in which the iodine occurs (58), (59), (216); according to some (53), (177) most of it is present as an organic compound soluble in water. The presence of iodides in the vacuoles can be demonstrated with cresyl blue ((39) p. 187, (40) p. 39, (126) p. 53, (148), (149)).

The localisation of iodine in special cells, such as is typical for diverse Florideae (p. 586), has not been observed in Phaeophyceae. On the other hand, the latter are distinguished by the liberation of iodine from the living alga under natural circumstances ((36-40), (43-46), (126) p. 78, (127), (231), (241) p. 66). This is very marked in certain seasons in the European species of *Laminaria*, as well as in *Ascophyllum nodosum* and *Pelvetia canaliculata*, less obvious in *Alaria* and in the species of *Fucus*; it takes place from the surface-layer ((36) p. 514, (37) p. 97) and is readily demonstrated by the blue colour assumed by starch-paste. Kylin ((126) p. 73) showed that the escape of iodine depends on the presence of 'iodide-oxidases' (cf. also (3), (189), (216) p. 88), which are believed to be located in the outer walls of the surface-cells ((44) p. 235, (46), (127) p. 206). In the presence of oxygen (cf. also (37) p. 111, (39) p. 218) and of an acid reaction in the membrane, these enzymes act upon the iodides that have diffused into the walls. The liberation of iodine must depend also on various causes affecting the degree of permeability of the cytoplasm of the surface-cells to the iodides of the sap. Liberation of iodine is in fact increased by immersion and exposure, by variations in temperature, wave-action, etc. (45). Regarding peroxidases, see (264).

The Nucleus

The nuclei of Phaeophyceae are usually large, their size being often closely related to that of the cell. Those of apical cells are commonly especially conspicuous and this is particularly marked in Sphacelariales, the nuclei of which have, as a consequence, been frequently investigated ((28) p. 10, (54), (66), (85) p. 347, (91), (234), (255)). A multinucleate condition is exceptional, although recorded in some Laminariales and in the older cells of *Halopteris*. The nuclei possess a large and readily stained nucleolus, and a delicate network, usually with little chromatic material (fig. 3, A, E), although obvious chromatin masses are reported in a few Fucales (fig. 3 F; (199) p. 170); some of the latter have nuclei with two nucleoli (fig. 3 F, *n*). The nucleoli are frequently vacuolate and this apparently becomes more marked during mitosis.

No other class of Algae affords such clear examples of *centrosomes*

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which, however, seem to be most readily demonstrated in the higher orders and in certain instances have only been recognised in the reproductive cells ((2), (152) p. 9). They are very conspicuous in the apical cells of Sphacelariales (fig. 3 B, *c*), in Dictyotales (fig. 3 A, *c*;

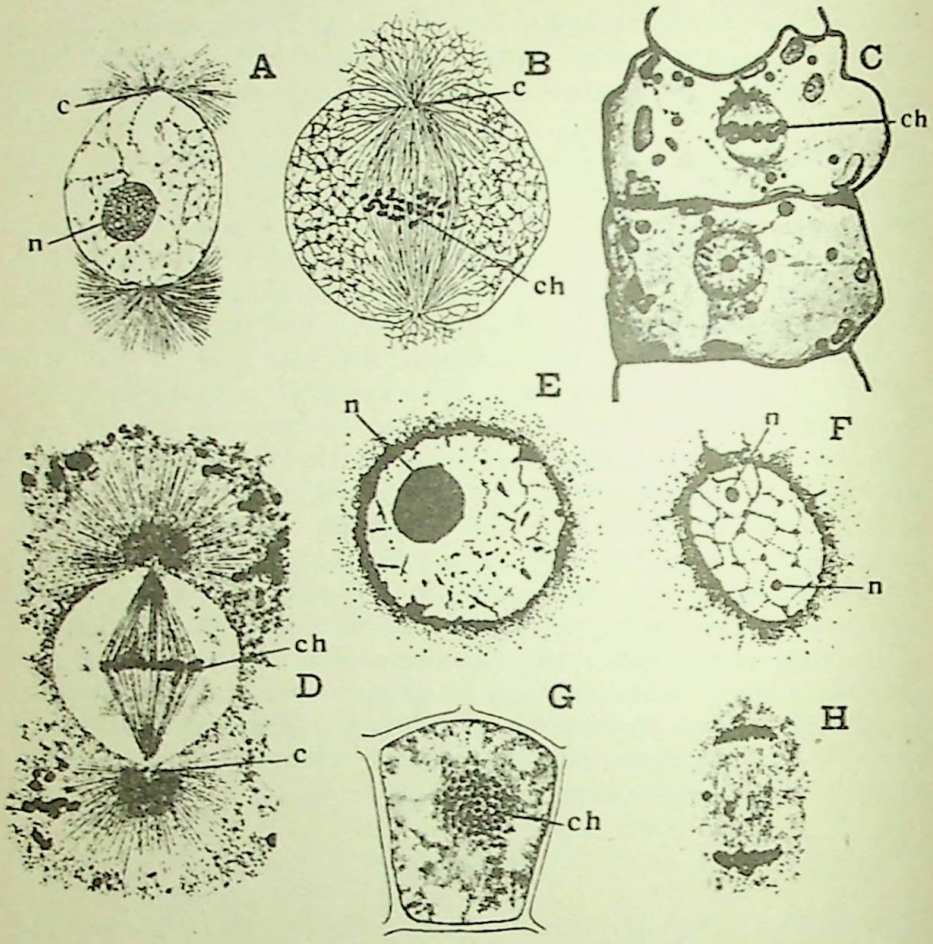

Fig. 3. Nuclei of Phaeophyceae. A, *Dictyota dichotoma* (Huds.) Lamour. B, *Halopteris scoparia* (Kütz.) Sauv., metaphase. C, *Pylaiella littoralis* (L.) Kjellm., upper nucleus in metaphase. D, G, H, *Fucus vesiculosus* L.; D, metaphase; G, polar view of anaphase; H, late anaphase. E, *Bifurcaria tuberculata* Stackh. F, *Fucus lutarius* Kütz. *c*, centrosome; *ch*, chromosomes; *n*, nucleolus. (A after Mottier; B after Escoyez; C after Knight; E, F after Roy; the rest after Yamanouchi.)

(16) p. 144, (166), (167) p. 170), and in Fucales (fig. 3 D, *c*; (176), (199) p. 176, (252) p. 175). The centrosomes, which are commonly described as rod-shaped, always lie in close contact with the nuclear membrane and are usually the centre of cytoplasmic radiations (fig. 3 A, B, D) which have sometimes alone been observed ((79) p. 242, (85) p. 348); in Cutleriales ((253) p. 448, (254) p. 4) and in certain other instances

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((28) p. 11) they have only been recognised at metaphase. According to Zimmermann ((255) p. 121) the radiations around the centrosomes of *Sphacelaria* arise through a reorientation of the cytoplasmic lamellae between the alveoli, which is accompanied by an increase in viscosity; this definite orientation is lost during metaphase.

At the commencement of mitosis the nucleus usually enlarges and two centrosomes with accompanying radiations become visible (fig. 3 A). It is still a matter of debate whether the second centrosome arises by division (167), (234) or *de novo* (54); according to Georgevitch (66) it is intranuclear in origin and derived from the fragmenting nucleolus. During prophase the chromatin in the outer nucleus increases in amount and gradually aggregates to form the small chromosomes; simultaneously the nucleolus stains less deeply and becomes more evidently vacuolate, although as a general rule persisting up to metaphase. Diverse earlier workers ((54) p. 189, (167) p. 173) concluded that the nucleolus contributed material for the development of the chromosomes, but this is unlikely. Spireme-like stages have occasionally been reported ((16) p. 144, (28) p. 10, (167) p. 175, (248) p. 143). The spindle always appears to be intranuclear (fig. 3 B–D); the nuclear membrane is in fact very persistent, except at the poles, where the fibres of the spindle converge on the centrosomes (fig. 3 B). When aggregated on the equatorial plate, the chromosomes are rounded or slightly elongated (fig. 3 B–D, G, *ch*). There is often a considerable contraction of the nucleus at metaphase. The cell-plate is formed by arrangement in one plane of the cytoplasmic lamellae between the alveoli ((31) p. 453, (167) p. 181, (234), (252) p. 179, (255) p. 126). There is never any relation to the nuclear spindle.

The reduction division, which except in Fucales is always located in the unilocular sporangium,[1] presents no special features. A distinct spireme stage is mostly recorded, followed by often long-continued synezesis and diakinesis (figs. 54 B–D; 89 G–I; pp. 164, 246). Centrosomes have usually been observed and the spindles are intranuclear. The haploid number of chromosomes is given as: 8–10 in Ectocarpales, although Abe (2) states that the number is 20 in *Heterochordaria*; usually 16 in Sphacelariales and Dictyotales; 13–15 in Laminariales; 24 in Cutleriales. In Fucales Yamanouchi and most recent workers ((1), (96) p. 12, (175), (235)) report 32 chromosomes, and the lower numbers given for *Sargassum* by Kunieda (115), as well as by earlier investigators (cf. (107) p. 186), are probably erroneous. The data suggest that there may be a greater measure of uniformity than is at present apparent.

The General Facts of Reproduction

Except for the Dictyotales and Fucales, all Brown Algae[2] reproduce by zoospores produced in definite sporangia, which are borne on the diploid phase. Among Ectocarpales and Sphacelariales there are

[1] See (1), (16) p. 146, (28) p. 12, (85) p. 350, (89) p. 35, (108) p. 350, (109) p. 314, (152) pp. 10, 27, (248) p. 145, (252) p. 179, (253) p. 469, (254) p. 21, (266) p. 677.

[2] The Tilopteridales, which show special features, not yet clearly understood (see p. 153), are omitted from this general consideration.

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commonly two kinds of sporangia, spoken of as *unilocular* and *plurilocular* respectively, but in all other zoosporic Phaeophyceae only the unilocular sporangium is represented on the diploid plant. This sporangium, as the name implies, is not partitioned (fig. 4 B, C, *u*), and the more or less numerous motile elements produced within it are formed simultaneously, after completed nuclear division, by separation of the cytoplasm into as many uninucleate portions (figs. 43 A–D; 89 A–F). The sporophytes of Dictyotales possess a special type of unilocular sporangium (*tetrasporangium*, fig. 108 G) producing usually four motionless spores. Meiosis in all Brown Algae, except Fucales, is associated with the first nuclear divisions in the unilocular sporangium so that the spores derived from it are normally haploid.

The plurilocular sporangium, on the other hand, is divided by transverse, and often also by longitudinal, septa (fig. 4 A, H, *p*) into numerous small compartments, each forming a single swarmer. No reduction occurs during the differentiation of the plurilocular sporangium and the zoospores it produces are therefore diploid. In the more advanced Ectocarpales and Sphacelariales such sporangia are commonly rare or lacking on the diploid phase, an indication of the evolutionary trend that has resulted in their complete disappearance in the sporophytes of the other zoosporic orders (Cutleriales, Desmarestiales, Laminariales).

The zoospores from the unilocular sporangia produce haploid gametophytic stages (figs. 4 F; 47 F–H), while those from the plurilocular sporangia constitute an accessory means of reproduction of the diploid phase. The gametophytic stages in the less specialised Phaeophyceae (Ectocarpales, Cutleriales, Sphacelariales) bear reproductive organs, in general character altogether identical with the plurilocular sporangia of the diploid phase, although unilocular sporangia are never present. The plurilocular sporangia of the haploid phase are, however, gametangia, and their swarmers, identical in form with those of the diploid phase, behave as gametes, although frequent apogamy occurs, at least in artificial cultures. The complete similarity of the gametangia of the haploid, and of the plurilocular sporangia of the diploid, phases long encumbered the elucidation of the life-cycle of Ectocarpales.

In most Ectocarpales, and probably also in many Sphacelariales (p. 291), the fusing gametes are morphologically identical, but pronounced anisogamy is found in a limited number of Ectocarpales (p. 122), as well as in Cutleriales (fig. 53 F). All other Phaeophyceae exhibit oogamy, usually with the production of a single ovum in the oogonium, although a few Fucales produce several (cf. p. 370). The ova are almost invariably extruded prior to fertilisation. The male cells, always motile, are commonly produced singly in the antheridia (Desmarestiales, fig. 62 K, L; Laminariales, fig. 4 F, *s*), although in Dictyotales (fig. 112 B, F) the male organ has the form of a pluri-

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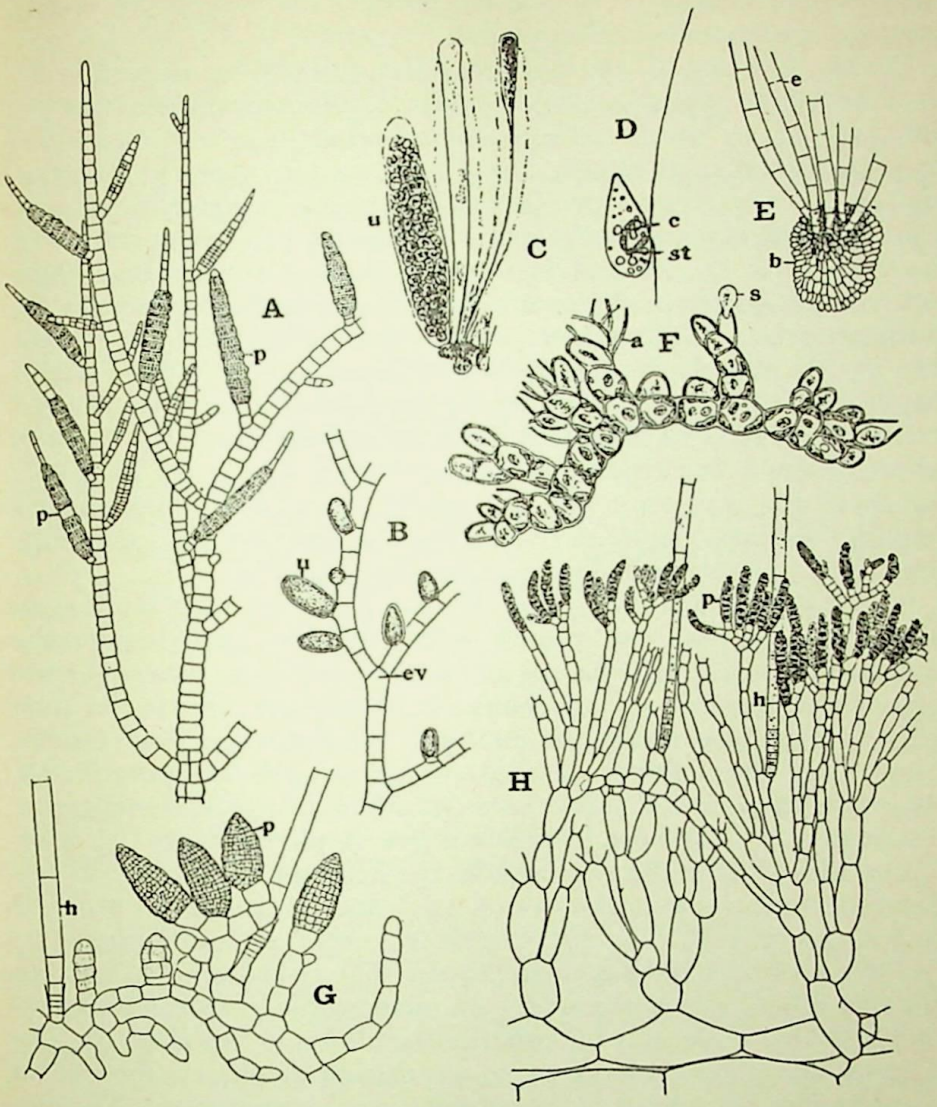

Fig. 4. Reproduction of Phaeophyceae. A, *Pylaiella littoralis* (L.) Kjellm., with plurilocular sporangia. B, *Ectocarpus confervoides* (Roth) Le Jol., with unilocular sporangia. C, *Saccorhiza bulbosa* De la Pyl., mature unilocular sporangium and two paraphyses. D, *Laminaria saccharina* (L.) Lamour., zoospore. E, *Ectocarpus subcorymbosus* Farl., basal part of a plant. F, *Alaria crassifolia* Kjellm., male prothallus. G, *Ectocarpus reptans* Crouan, with plurilocular sporangia. H, *Castagnea contorta* Thur., with plurilocular sporangia. *a*, antheridium; *b*, basal system; *c*, chromatophore; *e*, erect system; *ev*, point of evection; *h*, hair; *p*, plurilocular and *u*, unilocular sporangium; *s*, spermatozoid; *st*, stigma. (C after Thuret; D, H after Kuckuck; F after Kanda; the rest after Taylor.)

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locular sporangium and in Fucales considerable numbers of spermatozoids are produced in the antheridium. The zygote invariably germinates without a resting period.

The motile cells (26), whether zoospores, gametes or spermatozoids, are of a uniform type (fig. 4 D). The two flagella are attached laterally, commonly rather nearer to the posterior end of the pear-shaped body; they are of unequal length, the longer usually directed forwards (fig. 47 N), and the shorter backwards during movement (114), (222). The eye-spot is usually adjacent to the point of attachment of the flagella (fig. 4 D, *st*), and is directly apposed to the often single chromatophore or (in the spermatozoids of Fucales) represents the chromatophore itself; when several chromatophores are present (fig. 54 H), one bearing the eye-spot lies adjacent to the place of origin of the flagella. The tip of the longer flagellum often acts as a sucker when the swarmer settles on a substratum, while it commonly serves to attach the male to the female cell (cf. fig. 44 B). As already indicated the uniformity of the motile element in Phaeophyceae implies a common origin for the members of this class from unicellular organisms presenting these particular characteristics.

So far as the evidence goes, the life-cycle normally involves an alternation between two phases, with reduction in the unilocular sporangium. In Ectocarpaceae and a few other Ectocarpales the two phases are alike and the alternation is isomorphic; this is also so in Dictyotales, *Zanardinia*, and probably all Sphacelariales. On the other hand the majority of Ectocarpales, as well as Sporochnales, Desmarestiales, and Laminariales, exhibit a marked heteromorphic alternation, with minute filamentous gametophytic stages (fig. 4 F). It is evident that in the Ectocarpales the heteromorphic alternation is derived from an isomorphic one (p. 127), and this is likewise probable in *Cutleria* (p. 169). There is, moreover, every reason to suppose that in Desmarestiales and Laminariales also the marked contrast between the two generations is secondary. In other words isomorphic alternation probably represents the primitive condition in this class (258). The Fucales afford no evidence of an alternation of phases, the diploid plant bearing sex organs as the only organs of reproduction. The life-cycle is here probably a highly derived one, the elucidation of which presents many difficulties (cf. p. 380).

Classification and Status of Phaeophyceae

Most of the orders of Phaeophyceae have long been recognised and are so clearly defined that there is no difference of opinion about their delimitation. Since a better knowledge of the life-cycle of the simpler Brown Algae has become available, rather diverse views have, however, been expressed as to their classification and still another grouping is adopted here. The reasons for this attitude are given on p. 138, where

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also some of the other schemes are discussed. The old subdivisions ((104) p. 180)—Phaeosporeae, Acinetae, and Cyclosporeae—can now scarcely be maintained. With few modifications the following nine orders in which I group the Phaeophyceae correspond to those of Oltmanns (179):

I. *Ectocarpales.* Filamentous or bulky pseudo-parenchymatous (uni- or multiaxial) or true parenchymatous types showing an obvious derivation from a heterotrichous filament; growth for the most part intercalary; asexual reproduction by zoospores from unilocular and plurilocular sporangia, sexual reproduction mostly isogamous, rarely anisogamous; alternation isomorphic or more commonly heteromorphic.

II. *Tilopteridales.* A problematic group of heterotrichous filamentous forms with intercalary growth; asexual reproduction by zoospores from unilocular (and plurilocular?) sporangia, as well as by "monospores"; sexual reproduction possibly anisogamous; alternation probably isomorphic.

III. *Cutleriales.* Thallus composed of congenitally fused threads, with trichothallic growth; isomorphic or heteromorphic alternation, the diploid phase reproducing by zoospores formed in unilocular sporangia, the haploid phase with plurilocular gametangia showing marked anisogamy.

IV. *Sporochnales.* Forms with bulky and complex thalli derived from a primary uniaxial construction; growth intercalary; asexual reproduction by zoospores formed in unilocular sporangia; sexual reproduction probably oogamous; alternation heteromorphic.

V. *Desmarestiales.* Uniaxial forms with complex cortication and intercalary growth; asexual reproduction by zoospores formed in unilocular sporangia; sexual reproduction oogamous; alternation heteromorphic.

VI. *Laminariales.* Bulky parenchymatous forms, mostly of large dimensions, with considerable morphological and anatomical differentiation; growth intercalary; asexual reproduction by zoospores formed in unilocular sporangia; sexual reproduction oogamous; heteromorphic alternation.

VII. *Sphacelariales.* Relatively small parenchymatous forms showing evident heterotrichy; apical growth; asexual reproduction by zoospores formed in unilocular sporangia; sexual reproduction isogamous (and oogamous?); isomorphic alternation probable.

VIII. *Dictyotales.* Little differentiated parenchymatous forms, often with dichotomous branching; apical growth; asexual reproduction by motionless tetraspores formed in a unilocular sporangium; sexual reproduction oogamous; alternation isomorphic.

IX. *Fucales.* Parenchymatous forms with complex morphological and anatomical differentiation; apical growth; no asexual reproduction; sex organs borne in conceptacles on the diploid phase and exhibiting meiosis during the formation of the sexual cells; no evident alternation.

The Phaeophyceae present no obvious affinities with any other class and are indeed in most respects so sharply circumscribed that

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little opportunity is afforded for speculations on their relationships. The possible similarity in pigmentation with Bacillariophyceae (Diatoms) is, if it exists, the only point of resemblance. The suggested derivation from Xanthophyceae ((49) p. 162) is based on incorrect assumptions. Various earlier authorities have sought an affinity between Dictyotales and Florideae on the grounds of the presence of motionless tetraspores in both and the supposed immobility of the spermatozoids in the former. Neither argument has, however, stood the test, since there is evidence to show that the Dictyotaceous tetrasporangium is a special form of the ubiquitous unilocular sporangium, while Lloyd Williams has demonstrated that the spermatozoids conform to the motile type of other Phaeophyceae.

On present evidence this class must be regarded as an altogether distinct evolutionary line (Phaeophyta). Its many approximations in morphological and anatomical respects (foliar differentiation, axillary branching, conducting system with sieve-tubes, secondary growth) to higher plants are no doubt but an expression of the general evolutionary trend within the plant-kingdom. As such and as examples of parallelism they are of the greatest possible interest, but they are undoubtedly without any direct phylogenetic significance. Attention may be drawn to the fact that similar specialisations are encountered also in Florideae with their altogether different basic construction and highly distinctive reproduction.

Among the few fossil types that have been ascribed to Phaeophyceae the most striking is *Prototaxites* (*Nematophycus*, *Nematophyton* (111), (137), (138) p. 259, (219) p. 192) from the Silurian and Devonian. The remains, some of which reach a diameter of 1 metre, consist of loosely aggregated forked threads, sometimes interwoven with much narrower ones (hyphae?). Periodic differences in the thickness of the walls of the threads occasionally give the appearance of growth-rings. In certain specimens ((100) p. 885) threads running perpendicular to the medullary region have been recognised. This form appears to have a multiaxial construction and might represent a large member of Ectocarpales; since there is no true parenchymatous structure, a reference to Laminariales ((111), (183) p. 95) cannot be supported. Lang ((138) p. 287) points out that there is no satisfactory evidence that *Prototaxites* is a member of Phaeophyceae or that it was an aquatic type.

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Order I. *ECTOCARPALES*

The numerous seaweeds grouped in this order have long been recognised as a coherent entity, though with increased knowledge of the processes of reproduction and of the course of the life-cycle diverse views as to their taxonomic arrangement have been formulated. The delimitation here adopted corresponds in many respects with the Ectocarpales of Oltmanns (182), although he included in the latter the Sporochnales and Desmarestiales, which are now regarded as constituting separate orders.

GENERAL CHARACTERISTICS

The Ectocarpales as thus delimited include the least specialised members of the Brown Algae and present a wide diversity of structure, ranging from the simple filamentous types of the Ectocarpaceae to

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relatively elaborate thalli. The latter are produced either by aggregations of filaments and of their branches (multiaxial as in *Leathesia*, fig. 17 and *Castagnea*, figs. 20, 21; uniaxial as in *Spermatochnus*, fig. 27) or are formed by the repeated subdivision of the cells of primary erect filaments (parenchymatous types like *Punctaria*, fig. 31, and *Scytosiphon*, fig. 34). Despite the considerable range in outward form and internal structure of the mature sporophytes, the younger stages of nearly all Ectocarpales show a clear derivation from the heterotrichous filament seen in *Ectocarpus* and other Ectocarpaceae. Development commences with the production of a system of prostrate filaments (figs. 17 E; 20 D) from which a number of upright branches sooner or later arise (fig. 31 A); one or more of the latter develop further to produce the mature plant (fig. 34 B, C). In other words the thallus, in all advanced Ectocarpales, is an elaboration of the erect threads of a primary heterotrichous stage. The growth of the thallus is diffuse or often accomplished by well-defined intercalary meristems (figs. 5 D; 14 B, *m*), but apical growth is met with in certain advanced forms.

Many Ectocarpales bear colourless multicellular hairs ((171) p. 77) which commonly grow with the help of a basal meristem (figs. 9 E, H; 16 C, D, *h*). A production of hairs seems to be a general characteristic of the primitive heterotrichous forms, being seen also in the Chaetophorales (1, p. 249) and in the Nemalionales among Red Algae, although the type of hair is variable. In the Ectocarpaceae the hairs usually terminate the branches of the filaments (fig. 5 D, *h*), whilst in the more elaborate Ectocarpales they either occur scattered (fig. 27) or united into characteristic groups (fig. 35 D), which are sometimes sunk in cavities (fig. 40 E). In some genera, especially among Myrionemataceae, the hairs are provided with a basal sheath[1] (fig. 9 E, H). Very similar to the colourless hairs are the structures (assimilatory hairs) found in *Elachista* (fig. 13 A) and its immediate allies, in which the cells contain chromatophores. It can hardly be doubted that the two are homologous, although it is at present not clear which is the more primitive.

Berthold ((28) p. 677; cf. also (178) p. 434) was of the opinion that the colourless hairs serve as a light-screen, whilst others ((180) p. 48, (183) p. 390, (214) p. 57, (220) p. 207, (292) p. 37) have regarded them as structures serving mainly for the absorption of mineral nutriment and for gaseous exchange. The degree of development of the hairs is very variable, but little is known of the conditions that determine this; Kylin ((151) p. 12) found that germlings of *Stilophora rhizodes* and *Asperococcus bullosus* produced hairs only in those cultures in which the solution was changed daily. See also the discussion on the function of the hairs of Florideae (p. 450).

[1] Regarding its development, see (87) p. 4, (155) p. 27, (220) p. 204. The account of Parke ((187) p. 20) is erroneous ((246) p. 190).

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The typical life-cycle in the Ectocarpales comprises an alternation between diploid and haploid phases, either of which seems to be capable of indefinite propagation, the diploid by accessory swarmers, the haploid by apogamous gametes. Although diverse departures from this normal life-cycle are known to occur (p. 137), an alternation of phases is probably of wide occurrence. In the Ectocarpaceae this alternation is essentially isomorphic, but in most of the advanced Ectocarpales it is heteromorphic, the elaboration of the upright system of the primary heterotrichous stage affecting only the diploid phase (sporophyte), while the haploid one (gametophyte) remains a mere filament. In other words, the sporophyte has evolved, whilst the gametophyte remains at the simple level of the Ectocarpaceae. In a few specialised Ectocarpales, however, the alternation is seemingly isomorphic (p. 130), both phases having undergone elaboration.

Apart from the underlying heterotrichy, the Ectocarpales are characterised by asexual reproduction by zoospores and by a process of sexual reproduction which is for the most part isogamous, though there is usually a physiological distinction between the fusing gametes. This physiological anisogamy, which also commonly betrays itself in a different behaviour of the two gametes, is, in a small number of Ectocarpales (p. 122), accompanied by marked morphological differentiation, in certain instances leading to a state of anisogamy which is not far removed from true oogamy (fig. 46 E). So far, however, no example of sexual reproduction has become known among Ectocarpales in which the female cell is non-motile.

As in other Phaeophyceae, the reproductive cells are invariably produced in specially differentiated organs, the unilocular (fig. 5 B, *u*) and plurilocular sporangia (fig. 5 C, *p*). The former are always confined to the diploid phase and undergo meiosis during the formation of zoospores, so that the products of these zoospores are normally haploid and gametophytic. Plurilocular sporangia occur both on the diploid and haploid phases, being the only organs of reproduction found on the latter, where they constitute gametangia. The plurilocular sporangia of the diploid plant exhibit no reduction division in the production of their swarmers, which are therefore diploid and serve to propagate the phase upon which they occur. The two phases of the life-cycle thus contrast also in their reproductive organs, the haploid bearing only plurilocular, the diploid usually both pluri- and unilocular sporangia.

GEOGRAPHICAL DISTRIBUTION AND OCCURRENCE

The Ectocarpales attain their chief development, both as regards abundance of individuals and numbers of genera and species, on temperate and polar (115) shores. Many of the genera and species that occur in the colder seas of the Northern Hemisphere are, however,

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also recorded from the Mediterranean (40), (64), (98) and other warmer seas (33). In the actual Tropics, on the other hand, representatives of this order are relatively rare (cf. e.g. (32), (102)), although members of the Encoeliaceae (*Colpomenia*, *Hydroclathrus*, *Chnoospora*) are widespread and the genus *Ectocarpus* seems to be practically ubiquitous. Certain genera (e.g. *Myriogloea*, *Splachnidium*, *Scytothamnus*) appear to belong essentially to the Southern Hemisphere, although penetrating some way towards the Tropics, but information as to the distribution of the southern Ectocarpales is still rather fragmentary. *Coilodesme* is characteristic of the Pacific coast of North America, though a few species also occur in Japan; another widespread North Pacific type is *Heterochordaria*. Several genera (*Geminocarpus*, *Caepidium*) appear to be confined to the Antarctic.

The majority of the Ectocarpales are annuals, the diploid phases often being represented only for a few months in the year, while at other times they are lacking. During the period of absence they persist as minute filamentous sporo- or gametophytic stages (p. 132), although their mode of occurrence in nature is at present hardly known. The sporophytes in large part inhabit the lower part of the intertidal zone or the sublittoral region, but *Ralfsia*, some species of *Pylaiella*, *Elachista*, and *Punctaria*, as well as *Chordaria flagelliformis*, *Dictyosiphon foeniculaceus*, and *Scytosiphon Lomentaria*, are commonly met with in the upper part of the littoral (cf. (130)).

THE GENERAL FEATURES OF VEGETATIVE ORGANISATION

(*a*) The simple filamentous Types and their immediate derivatives (Ectocarpaceae)

Ectocarpus ((87) p. 14, (114) p. 34, (131), (132), (199) p. 21), with numerous species found especially in the colder seas, appears from every point of view to be the most primitive of living Brown Algae. The prostrate system of the heterotrichous filament (fig. 4 E; 5 J, *b*) is well marked in diverse species, although it is uncertain whether it occurs in all; as in other heterotrichous types, it evidently varies in its degree of development. The erect system not uncommonly, and perhaps typically, consists of but few erect, copiously branched filaments ((147) p. 8), but there would seem to be all gradations between this condition and that in which the prostrate base bears a more or less considerable number of little branched erect threads (figs. 4 G; 7 A) and itself constitutes an essential part of the vegetative system; such forms grade over to the reduced types considered below and to the Myrionemataceae (p. 60).

Species with well-branched erect threads form the brown tufts (fig. 5 A) which are familiar objects attached to the rocky sides of tidal pools and to other larger Algae, both in the littoral and sublittoral

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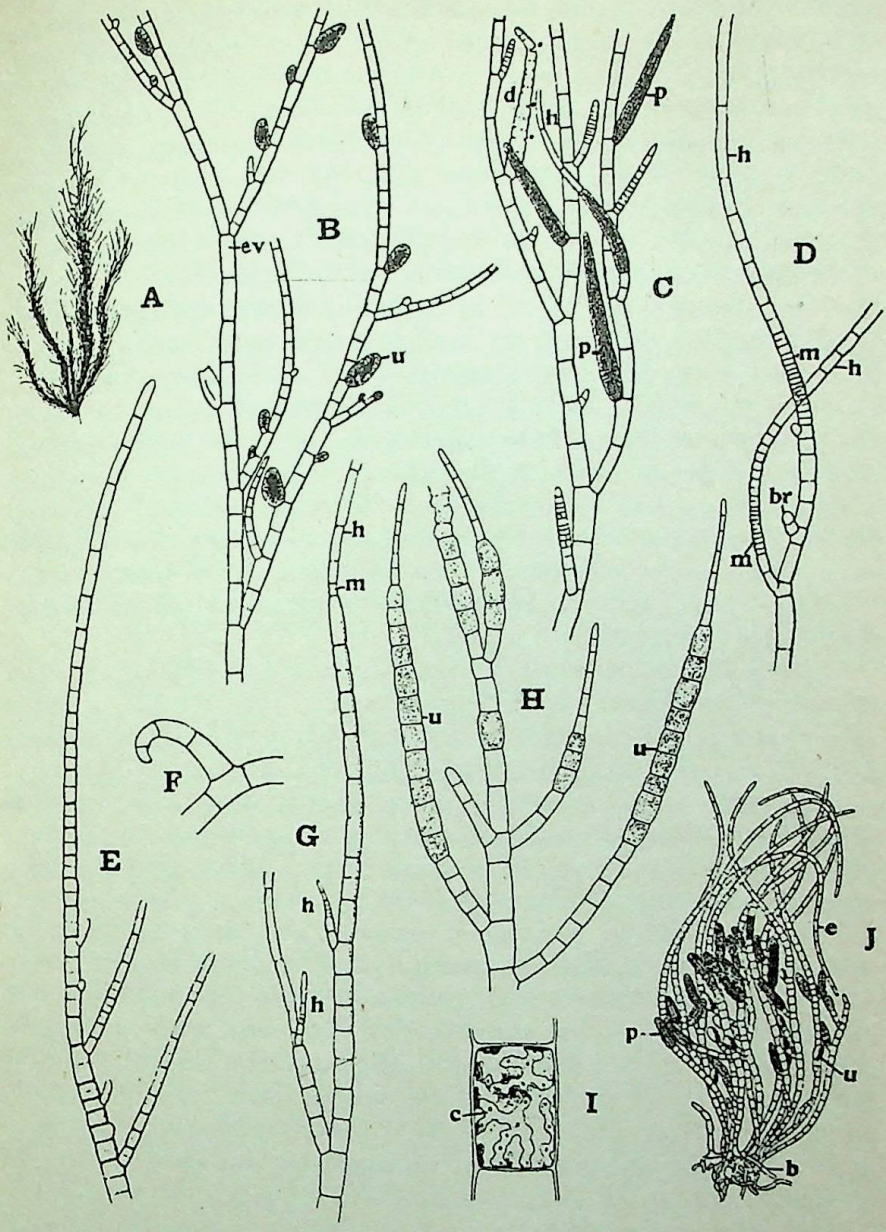

Fig. 5. *Ectocarpus* and *Pylaiella*. A, *Ectocarpus tomentosus* (Huds.) Lyngb., habit. B, C, E, I, *E. siliculosus* (Dillw.) Lyngb.; B with unilocular, and C with plurilocular sporangia; I, single cell. D, *E. irregularis* Kütz., trichothallic growth. F, *E. breviarticulatus* J. Ag., hooked branch. G, *E. criniger* Kuck. H, *Pylaiella littoralis* (L.) Kjellm., with unilocular sporangia. J, *Ectocarpus cylindricus* Saund., forma, heterotrichy. *b*, basal system; *br*, branch *c*, chromatophore; *d*, dehisced plurilocular sporangium; *e*, erect thread *ev*, point of evection; *h*, hair; *m*, intercalary meristem; *p*, plurilocular, and *u*, unilocular sporangium. (A, H, I after Taylor; F after Boergesen; J after Setchell & Gardner; the rest after Kuckuck.)

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regions. There is commonly a marked difference in size between the main axes and the later branches, which usually terminate either in a point (fig. 5 E) or in a series of elongate tapering cells, with few or no chromatophores, forming a hair (*E. siliculosus*). The branches arise from just beneath the septa (fig. 5 B, H) and frequently retain their lateral position, although evection (1, p. 234) may occur, resulting in apparent dichotomy (figs. 4 B, 5 B, *ev*). Attachment is commonly aided by the outgrowth of rhizoids from the lower cells of the main axis, and these may arise in such numbers as to form a basal cortication (e.g. *E. granulosus* C. Ag. (95) pl. 200). In several species the erect threads tend to coil around one another or to become matted together. The former condition is commonly seen in *E. fasciculatus* Harv. ((95) pl. 273) and *E. siliculosus*, while in *E. breviarticulatus* ((32) p. 173, (256) p. 429) and *E. tomentosus* ((95) pl. 182, (209))—the latter a frequent epiphyte on *Fucus*—the main filaments become twisted to form tufts, from 1–3 mm. thick (fig. 5 A), the individual strands of which are bound together by means of numerous short bent branches (fig. 5 F) or by rhizoid-like structures. This condition recalls that found in *Spongomorpha* (1, p. 237). Regeneration of wounded threads has been studied by Prowazek ((191) p. 746).

Growth of the prostrate system is apical, but that of the erect threads shows considerable diversity ((135) p. 179, (182) p. 6). Apical growth seems to be exceptional, although it is recorded in *E. lucifugus* Kuck. ((182) p. 8) and *E. chantransioides* S. & G. ((253) p. 406). In most species (e.g. *E. siliculosus*) the erect threads show diffuse growth (fig. 5 E), although in some instances (e.g. *E. granulosus*, cf. (182) p. 7) there may be localisation of division to certain places. Definite intercalary meristems are found only in a limited number of species (*E. paradoxus* Mont., *E. Lebelii* Crouan, *E. irregularis* Kütz., etc.) in which the entire growth of the individual branches is restricted to certain zones, each situated at the base of a hair (fig. 5 D). The cells of the meristem (*m*) cut off segments both above and below, the former, which are few, adding to the length of the terminal hair (*h*), while the latter give rise to ordinary photosynthetic cells from which also branches (*br*) are produced. This is the *trichothallic growth* ((106) p. 105) characteristic of diverse Ectocarpales, as well as of other orders of Brown Algae. Some species exhibiting this type of growth (e.g. *E. irregularis* (244) p. 103) also show occasional divisions in the main axes.

Hairs are by no means confined to the species possessing trichothallic growth, occurring also in some with diffuse growth (*E. siliculosus*). In certain of these (e.g. *E. criniger* (135) p. 178) the hairs are in part narrower than the underlying thread and originate from a well-defined basal meristem (fig. 5 G).

When the erect threads are well developed, the sporangia are terminal on short lateral branches or not uncommonly are sessile on

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the larger ones (fig. 5 B, C); in a few species (*E. irregularis* (244) p. 103; *E. coniferus* Boerg. (32) p. 167) they may appear in a pseudo-axillary position. The plurilocular sporangia are not infrequently surmounted by a few hair-cells (fig. 5 C). *Pylaiella*[1] ((37), (131) p. 3, (268) p. 101) has the same structure as *Ectocarpus*, except for a tendency to longitudinal division of the cells (fig. 4 A). It is characterised by the usual intercalary position of the sporangia (figs. 4 A; 5 H), the unilocular ones (*u*) occurring in short series. In the Pacific *P. Postelsiae* (259), in which only plurilocular sporangia are known, entire branches become converted into sporangia.

According to Kylin ((154) p. 3; cf. also (162) p. 32) the common *P. littoralis* includes two different species, the one an epiphyte for which this name is retained, the other essentially a lithophyte (*P. rupincola* (Aresch.) Kyl.), which is vegetatively distinguished by the coiling of the lower threads around one another; there are also differences in reproduction (p. 129). The rare *P. fulvescens* Bornet (37, 211) is distinguished by the loose felting together of the erect threads by means of numerous rhizoid-like branches (see also p. 27).

Several genera with well-developed erect threads show essentially the same vegetative features as *Ectocarpus*. *Pleurocladia lacustris* ((105) p. 114, (123), (291)), a rather rare freshwater form, is distinguished by the abundant deposition of carbonate of lime between the upright threads, which gives the minute, yellowish-brown cushions a certain rigidity. The numerous branches are short and tend to be unilateral (fig. 6 A); most of them ultimately bear unilocular (*u*) or plurilocular (fig. 6 C, *p*) sporangia. *Sorocarpus uvaeformis* Pringsh. ((1) p. 335, (45) p. 459, (119), (189)), a rare marine epiphyte, is characterised by bearing the small (plurilocular) sporangia (fig. 6 F, *p*) in grape-like clusters on short condensed branch-systems, usually situated at the base of a hair (see also (272)).

In the Mediterranean *Zosterocarpus* ((38); incl. *Prototilopteris* (75*a*) p. 359) the plurilocular sporangia form a peripheral girdle around a central cell from which they have been cut off by longitudinal walls (fig. 6 D, E, *p*). The genus is also distinguished by the position of the laterals opposite the septa (fig. 6 B) and the presence of enlarged fucosan-cells (*f*) with greyish contents (brown after death; (240) p. 89). Its affinities are obscure, but the longitudinal septation that occurs in the formation of the sporangia recalls the condition found in the polystichous Ectocarpales (p. 96), and *Zosterocarpus* is possibly a reduced member of that series. In *Geminocarpus* ((257) p. 12, (261) p. 9), based on the Antarctic *Ectocarpus geminatus* Hook. fil. et Harv. ((14) p. 16, (94) p. 469), there is frequent longitudinal septation, but the sporangia are dispersed on lateral branchlets as in an *Ectocarpus*; the branches are opposite.

In the species of *Ectocarpus* with short erect threads the sporangia may arise terminally upon them (*E. faeroensis* Boerg. (182) p. 13), but

[1] Sometimes spelt *Pilayella*.

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in others they are borne directly on the prostrate base (*E. elachistaeformis*, fig. 7 A; *E. Battersii*, fig. 7 B; (33) p. 36, (208)). The latter is then usually well developed and may branch so copiously as to become

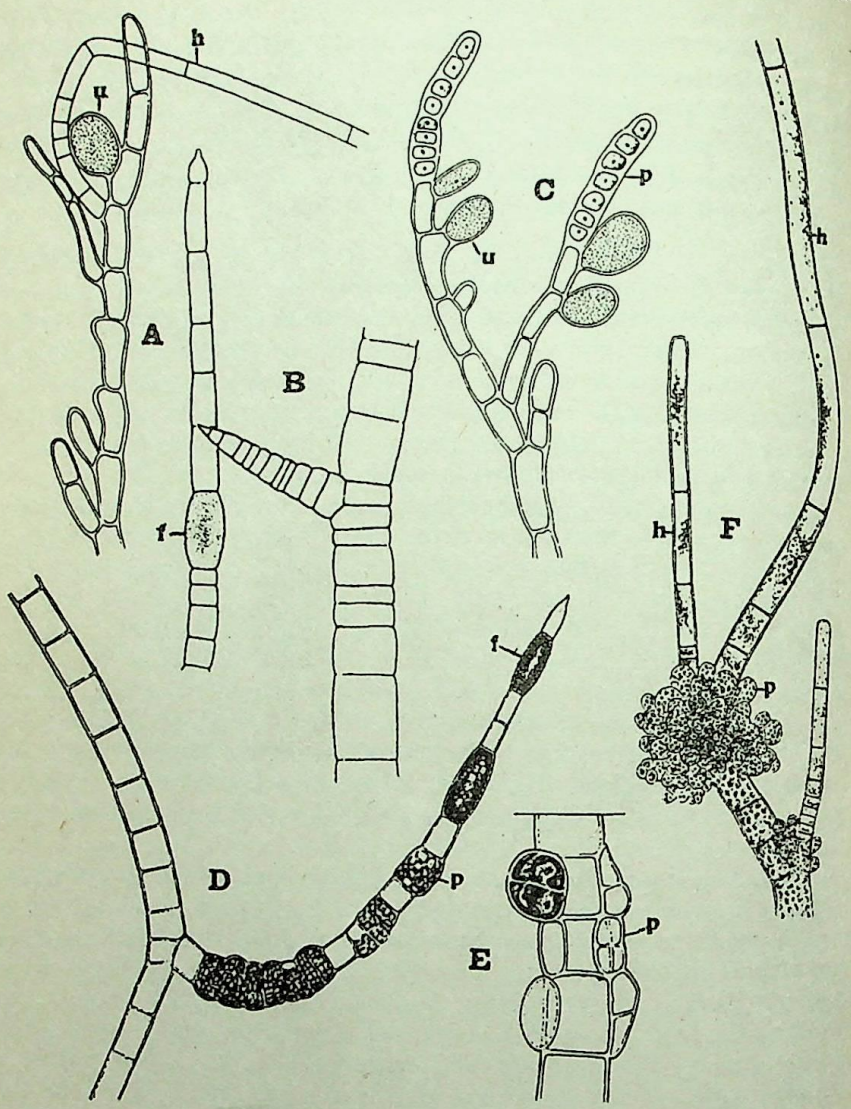

Fig. 6. A, C, *Pleurocladia lacustris* A. Br., erect threads, with the two kinds of sporangia. B, D, E, *Zosterocarpus Oedogonium* (Menegh.) Born.; B, threads showing mode of branching and fucosan-cell; D, E, threads with plurilocular sporangia. F, *Sorocarpus uvaeformis* Pringsh., with plurilocular sporangia. *f*, fucosan-cell; *h*, hair; *p*, plurilocular and *u*, unilocular sporangia. (A, C after Wille; B after Sauvageau; D, E after Bornet; F after Pringsheim.)

pseudo-parenchymatous (fig. 7 F, *b*). Apart from the fertile branches it may bear ordinary photosynthetic threads (*E. elachistaeformis*, fig. 7 A, *e*; (32) p. 174, (100) p. 470) which may exhibit a trichothallic

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meristem and terminate in long hairs (*E. Battersii*, fig. 7 B), or again there may be for the most part only hairs with a basal meristem (e.g. *E. speciosus* (182) p. 13). In *E. maculans* Kuck. ((133) p. 376), finally, the basal disc bears only plurilocular sporangia with unicellular

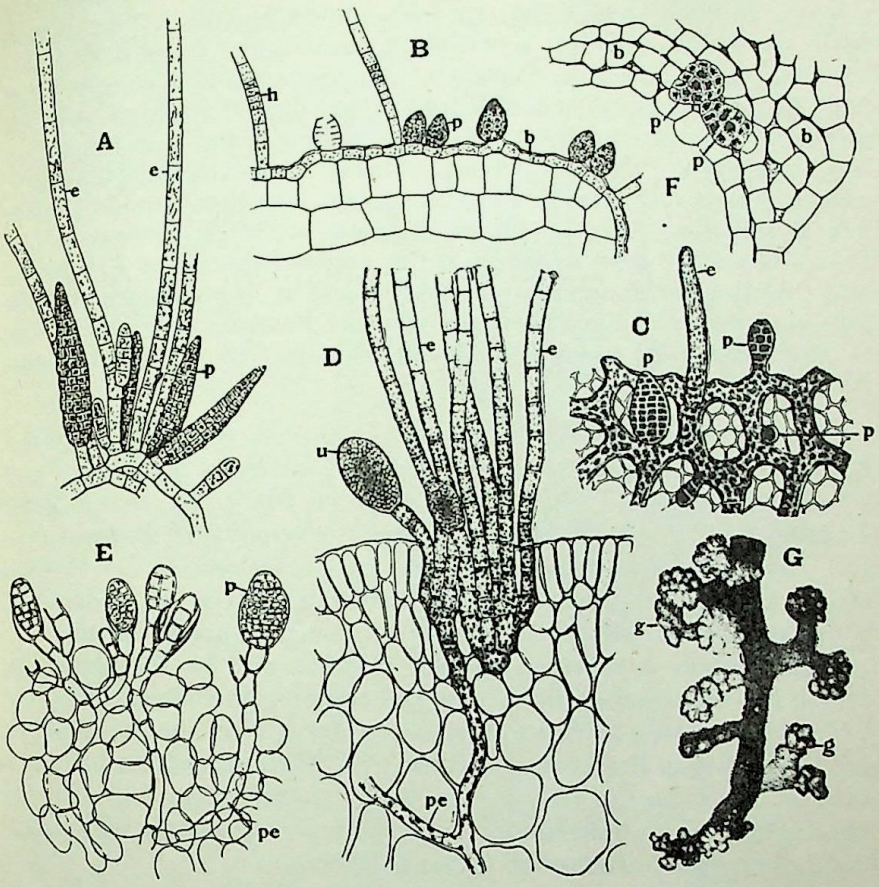

Fig. 7. A, B, D–F, Reduced species of *Ectocarpus*. A, *E. elachistaeformis* Heydr.; B, *E. Battersii* Born. var. *mediterranea* Born., on *Taonia*; D, *E. velutinus* (Grev.) Kütz. on *Himanthalia*; E, *E. Valiantei* Born. on *Cystoseira*; F, *E. maculans* Kuck., surface view of basal system. C, G, *Streblonemopsis irritans* Valiante; C, section of stratum; G, galls (*g*) on *Cystoseira ericoides* caused by the endophyte. *b*, basal system; *e*, erect thread; *h*, hair; *p*, plurilocular sporangium; *pe*, endophytic thread; *u*, unilocular sporangium. (A, B after Boergesen; C, G after Valiante; D, E after Sauvageau; F after Kuckuck.)

stalks (fig. 7 F, *p*). There is evidently considerable variation even in one and the same species; thus, although the erect threads are often unbranched, they may occasionally show some ramification and bear the sporangia laterally (cf. (33) p. 36).

Several species of *Ectocarpus* ((207); cf. also (85), (179) p. 212) have their basal filaments endophytic in (and perhaps to some extent parasitic

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upon) the tissues of diverse larger Algae. The endophytic threads penetrate in all directions within the gelatinous walls of the substratum, often causing some distortion and sometimes extending to appreciable depths (fig. 7 D, *pe*); *E. Valiantei* (fig. 7 E) produces galls on *Cystoseira* ((207) p. 57) and *E. deformans* Dang. on *Laminaria* (57). The endophytic threads, however, retain their chromatophores and do not in general enter the cells, although according to Sauvageau ((207) p. 78) this happens in *E. minimus*. Certain of the species under consideration (e.g. *E. luteolus* Sauv.; cf. also (159) p. 40) exhibit multiplication by means of threads that extend over the surface of the host and set up fresh infections. Others, which are probably more extreme "parasites", ramify extensively within the host before any considerable growth develops at the surface (*E. parasiticus* Sauv. (20) p. 51, (57), (207) p. 92). It is noteworthy that, in many of the reduced species of *Ectocarpus*, only plurilocular sporangia are known, and it is possible that some represent stages in the life-history of other Ectocarpales. Hamel ((87) p. xxiv) refers *E. parasiticus* and *E. maculans* to a separate genus *Entonema*.

It is scarcely possible ((198) p. 41, (207) p. 5, (256) p. 408) to draw a hard and fast line between the reduced forms of *Ectocarpus* and *Streblonema* ((47), (71), (149) p. 49, (150) p. 11, (189) p. 13, (219) p. 271); Levring ((159) p. 38), in fact, advocates the removal of *E. parasiticus* (cf. above) to this genus. In the typical species of *Streblonema* (fig. 8 C, I, L) the plant consists almost wholly of the endophytic prostrate system, which consists of a loosely branched thread. The upright system is represented only by hairs and by the sporangia, which are often borne directly on the creeping threads and may not project beyond the surface of the host. A freshwater species epiphytic on *Compsopogon* has been described (12). More marked reduction is evident in *Bodanella* ((77) p. 101, (298)), a lithophyte found in the continental lakes; here there is only the creeping system with unilocular sporangia borne on its upper surface.

It is not altogether easy to demarcate *Phaeostroma* ((30) p. 441, (135) p. 182, (162) p. 24, (203) p. 68) from *Streblonema*. *S. aequale* Oltm.[1] ((179) p. 214), regarded by Kuckuck ((134) p. 385) as belonging to the former genus, is nowadays usually retained in *Streblonema* ((87) p. 69, (162) p. 30).

One of the simplest of the prostrate and probably reduced Ectocarpaceae is *Mikrosyphar* ((24), (134) p. 380, (135) p. 177, (136)), an endophyte in *Zostera* and in Red Algae. *M. Polysiphoniae* (fig. 8 A) occupies a subcuticular position within its host, whereas *M. Porphyrae* (fig. 8 K) develops numerous penetrating threads traversing the walls and extending from face to face of the *Porphyra*-thallus; there are also some projecting hairs (*h*). Swarmers are liberated singly from the cells of

[1] This species was first found on *Chorda* by Buffham (42), who, however, regarded its plurilocular sporangia as belonging to the host (cf. (134) p. 386).

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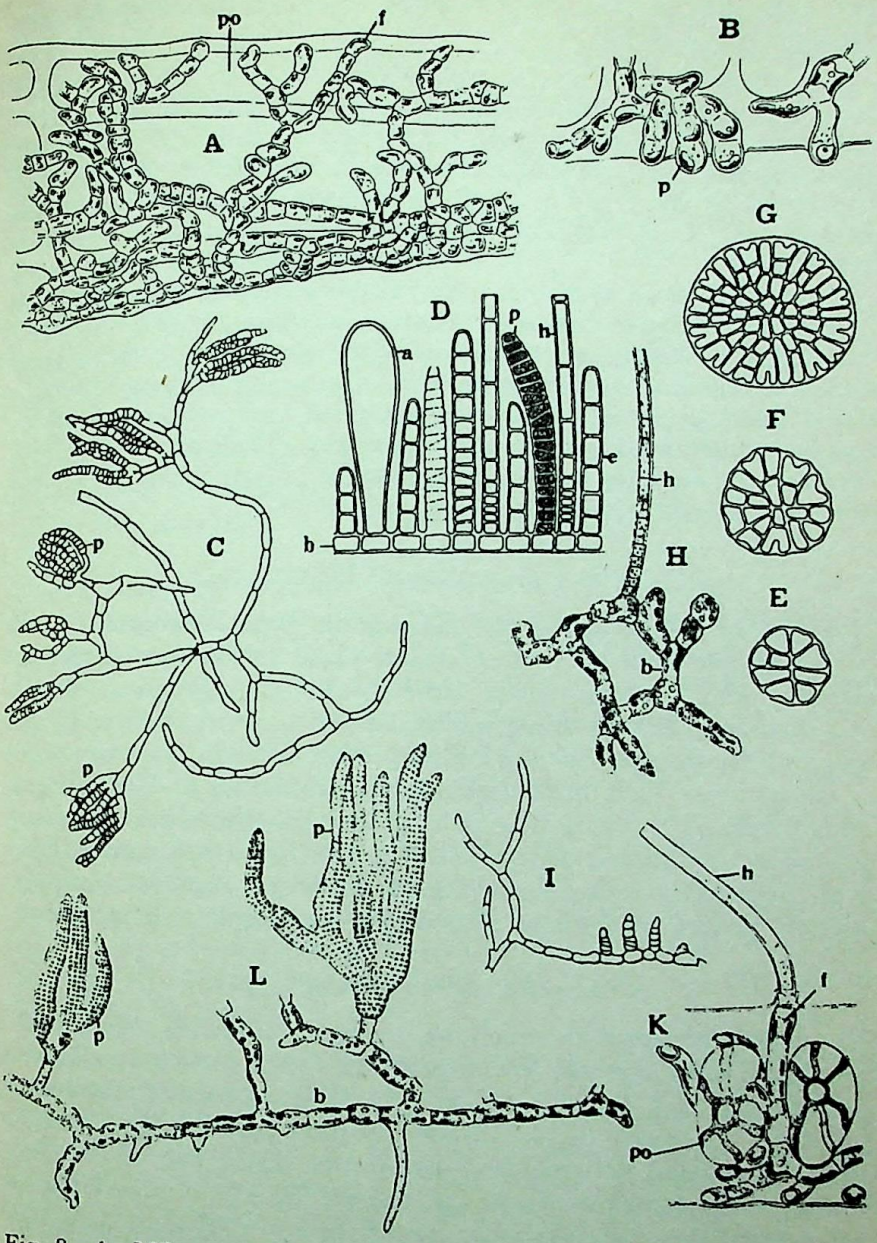

Fig. 8. A, *Mikrosyphar Polysiphoniae* Kuck. B, K, *M. Porphyrae* Kuck.; B, threads from the surface; K, section of *Porphyra* (*po*) showing endophytic threads. C, I, *Streblonema corymbiferum* Setch. & Gardn. D–G, *Ascocyclus orbicularis* Magnus; D, section of mature disc; E–G, developing discs. H, L, *Streblonema volubilis* Pringsh. *a*, ascocyst; *b*, basal system; *e*, erect thread; *f*, endophytic thread; *h*, hair; *p*, plurilocular sporangia; *po*, host. (A, B, K after Kuckuck; C, I after Setchell & Gardner; D–G after Kylin; H, L after Pringsheim.)

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short 2–4-celled laterals, which Kuckuck regards as simple plurilocular sporangia (fig. 8 B, *p*).

A more markedly parasitic type is constituted by *Streblonemopsis* ((207) p. 100, (287)), the branched threads of which, anastomosing to form a network (fig. 7 C), occur within the surface of small richly lobed galls (fig. 7 G) on Mediterranean *Cystoseiras*; it is probable that the galls are caused by the presence of the endophyte. There are few upright threads (fig. 7 C, *e*). De Toni (285) would refer this genus to Reinsch's *Entonema*.

Ascocyclus[1] occurs as minute epiphytic discs, superficially resembling those of a *Coleochaete* and usually circular in outline (fig. 8 E–G). They bear (fig. 8 D) uniseriate plurilocular sporangia (*p*), hairs with a basal meristem (*h*), and long ascus-like cells (*a*) to which the genus owes its name. These ascocysts, when young, are filled with numerous fucosan-vesicles, while in older plants they are empty. Feldmann ((64) p. 256) has recently recorded unilocular sporangia. Many authorities place this genus among Myrionemataceae (cf. below).

(*b*) The Haplostichous Ectocarpales

The further evolution of the filamentous type illustrated by the Ectocarpaceae appears to have taken place in the two directions already referred to above, viz. either by the aggregation of threads and their branches affording multiaxial and uniaxial thalli or by the longitudinal septation of the primary erect threads. The two types of construction have been designated *haplostichous* and *polystichous* respectively by Kuckuck ((147) p. 6, (182) p. 5), and they are considered separately as a matter of convenience. The two series do not, however, necessarily represent divergent lines, and some of the polystichous genera are perhaps related to certain haplostichous forms.

Crust- and cushion-forming Types

Those Ectocarpaceae, in which the prostrate base bears several little-developed erect threads, lead over to the forms included in Myrionemataceae ((159) p. 48, (256) p. 453). The species of *Myrionema* ((6) p. 53, (25), (149) p. 34, (220)) are for the most part epiphytes forming minute, rounded or irregular, olive-brown discs; one of the commonest is *M. strangulans* Grev. (*M. vulgare* Thur.), found on Ulvaceae and other Algae. *M. aecidioides* Sauv.[2] ((220) p. 177) is an endophyte

[1] See (48), (64) p. 251, (97) p. 243, (149) p. 39, (162) p. 40, (166) p. 73, (199) p. 19, (220) p. 274, (268) p. 107. With reference to the nomenclature of the species of this genus, see (64) p. 251, (152) p. 22, (231) p. 13.

[2] *Ectocarpus aecidioides* ((23), (70) p. 136, (202) p. 894); *Phycocoelis aecidioides* Kuck. ((133) p. 234). The species of the genus *Phycocoelis*, established by Strömfelt (264), are in part referred to *Myrionema* ((220) p. 170), in part to *Ascocyclus* ((52) p. 122), while *P. maculans* Collins ((45) p. 459) is *Hecatonema maculans* Sauv., which Levring ((159) p. 45, (162) p. 36) refers to *H. terminalis* (Kütz.) Kyl.

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in *Laminaria*. In *M. strangulans* (cf. also (284)) and other species there is a compact one-layered basal stratum (fig. 9 A, B), which represents the first-formed part of the plant; it exhibits marginal growth and consists of clearly distinguishable radiating threads which show pseudo-dichotomous branching. In older individuals only the peripheral parts are directly attached to the substratum, while the central cells may produce rhizoids (fig. 9 C, J, *r*) of diverse length ((220) p. 200). In *M. aecidioides* the prostrate system creeps beneath the surface layer of the host, and a compact disc is only formed when the plant becomes fertile (fig. 9 F).

Except in the marginal growing region nearly every cell of the basal stratum produces an erect thread. The majority of these upgrowths take the form of short simple (or rarely once-branched) photosynthetic threads (fig. 9 C, *e*) which, though compactly aggregated and sometimes enclosed in common mucilage,[1] are not laterally fused. As a general rule these erect filaments develop progressively from the centre outwards (fig. 9 E) and attain to a uniform height; their growth is largely apical ((220) p. 209). In *M. siliquosum* ((246) p. 179) they are comparatively elongate and moniliform towards the summit. More or less plentiful colourless hairs (fig. 9 E, H, *h*), provided with a basal sheath and elongating by means of the usual basal meristem, project from among the photosynthetic threads. They usually originate directly from the cells of the prostrate system and develop earlier than the surrounding filaments (fig. 9 E).

The large unilocular sporangia are generally borne laterally on the basal cells of the photosynthetic threads (fig. 9 C, *u*), although in some individuals many arise directly from the basal stratum; such are sessile or supported on a one-celled stalk. The uniseriate plurilocular sporangia of *M. strangulans* usually show the latter disposition (fig. 9 J, *p*), although sometimes lateral on the erect threads. In some species (e.g. *M. patagonicum* Skottsb. (261) p. 18) the basal system bears hairs and sporangia only.

Other genera of Myrionemataceae show much the same structure. *Ulonema rhizophorum* Foslie ((23), (70) p. 131) is very similar to *Myrionema strangulans* ((220) p. 233) and is indeed included in that species by Levring ((159) p. 48, (162) p. 38). In *Hecatonema* ((48), (149) p. 39, (160) p. 45, (220) p. 248, (261) p. 15) the photosynthetic threads are of unequal height and in part of considerable length (fig. 9 D); moreover many of the cells in the outer part of the basal stratum produce no erect growths. Kylin ((154) p. 8) is no doubt right in including in this genus *Ectocarpus terminalis* Kütz. ((114) p. 54, (133) p. 376) which, in its sheathed hairs and other features, closely resembles the species of *Hecatonema* (cf. also

[1] This feature is more marked in *Microspongium* ((70) p. 130, (197) p. 20, (198) p. 46, (199) p. 11, (247) p. 156, (267)), where the growths are gelatinous. The base in this genus is two-layered and the erect threads are usually branched.

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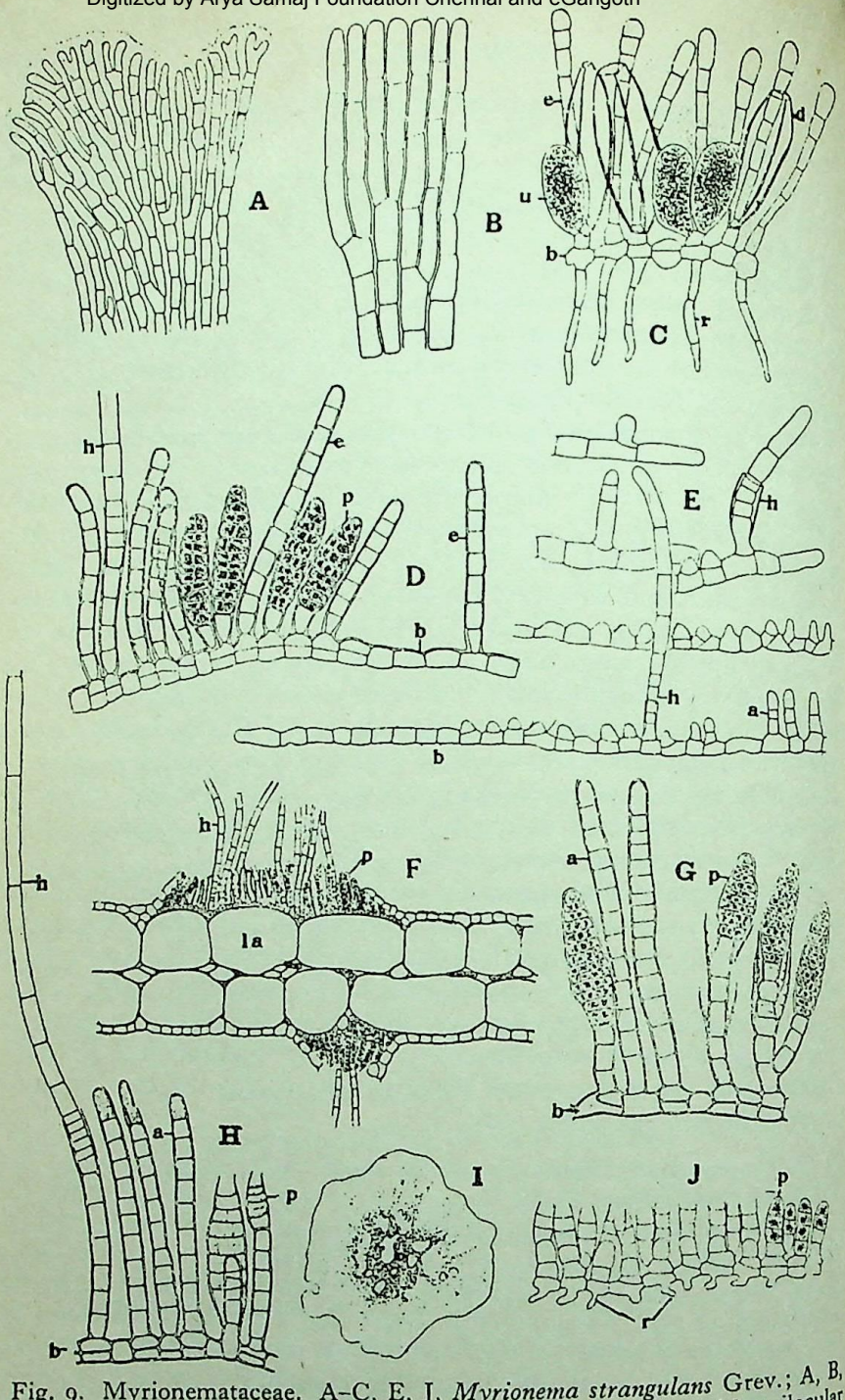

Fig. 9. Myrionemataceae. A–C, E, J, *Myrionema strangulans* Grev.; A, B, parts of basal system, in surface view; C, the same in section, with unilocular sporangia; E, development of hairs and of erect threads from the basal stratum; J, plurilocular sporangia. D, *Hecatonema maculans* Sauv., vertical section, with plurilocular sporangia. F, *Myrionema aecidioides* Sauv. on *Laminaria* (*la*), in vertical section. G–I, *Chilionema Nathaliae* Sauv.; G, H, vertical sections with photosynthetic threads and plurilocular sporangia; I, habit, from the surface. *a* and *e*, erect photosynthetic threads; *b*, basal stratum; *d*, dehisced unilocular sporangium; *h*, hair; *p*, plurilocular and *u*, unilocular sporangium; *r*, rhizoid. (B after Kylin; F after Kuckuck; the rest after Sauvageau.)

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(64) p. 261, (160) p. 45). Many of the latter, however, approach certain species of *Ectocarpus* rather closely.

In *Chilionema* ((25) p. 371, (220) p. 263) the basal stratum bears dense tufts separated by areas in which few or no erect growths are produced (fig. 9 G–I). Both in *Hecatonema* and *Chilionema*, which are closely related ((190) p. 139), the cells of the basal layer undergo horizontal division (fig. 9 D, G, H). Only plurilocular sporangia are known. *Compsonema* ((33) p. 59, (64) p. 258, (143), (247) p. 154, (256) p. 473), a lithophyte recorded from the Adriatic and the Canary Isles, would seem to belong to this affinity, despite the extensive development of the erect threads.

More distinctive types are constituted by *Petroderma* and *Nemoderma*. In the former ((134) p. 382), which has been recorded also from Clare Island ((52) p. 123), the elongate erect threads (fig. 10 H, *e*) are held together only by mucilage. Both types of sporangia are terminal. *Nemoderma* ((40) p. 241, (144)) forms small brownish gelatinous crusts in the littoral and upper sublittoral regions of warmer seas. It was first described from near Tangier in Morocco, but has since been found also in the Mediterranean ((64) p. 201, (65) p. 201, (222)) and in the Canary Isles (33). The one- to three-layered basal stratum (fig. 46 A, *b*) bears elongate upright threads (*e*), which are held together only by the gelatinisation of their walls; in the older crusts the lower cells contain few or no chromatophores and appear to serve for storage only. The abundant hairs are sunk in groups in the crusts, their basal meristem in later stages producing ordinary thallus-cells below. Unlike the forms previously discussed, the unilocular sporangia develop from intercalary cells in the upper parts of the threads (fig. 46 D, *u*), while the sex organs are borne laterally at about the same level (fig. 46 A, *ma*, *mi*), but on distinct individuals. The greater specialisation, evident in the structure of the thallus, as well as in the sexual process (p. 124), is also shown by the restriction of the reproductive organs to a special zone near the surface of the crust (cf. Elachistaceae).

A different development of the type of structure under consideration is found in *Ralfsia* ((31), (32) p. 190, (198) p. 48, (199) p. 9; incl. *Stragularia* Strömf. (69) p. 264), where the erect threads are coalescent (fig. 10 D, E, *e*). The species are perennials and form dark brown, almost black, often leathery crusts (fig. 11 A), frequent on rocks in the littoral region. The crusts are circular, although older ones often possess a lobed margin; they frequently show concentric zonation (fig. 11 A) and may attain to 15 cm. or more in diameter. Older ones often exhibit considerable differences in thickness and have a rather uneven surface. Adjacent crusts commonly overgrow one another so that a complex structure may appear in transverse section. The basal layer (fig. 10 F) is either attached directly to the rock (fig. 10 E) or by means of septate rhizoids (fig. 10 D, *r*), and every cell bears an upright thread. These threads show apical growth and frequently fork a little way above the base (fig. 10 D, *e*); in some species (e.g. *R. verrucosa*

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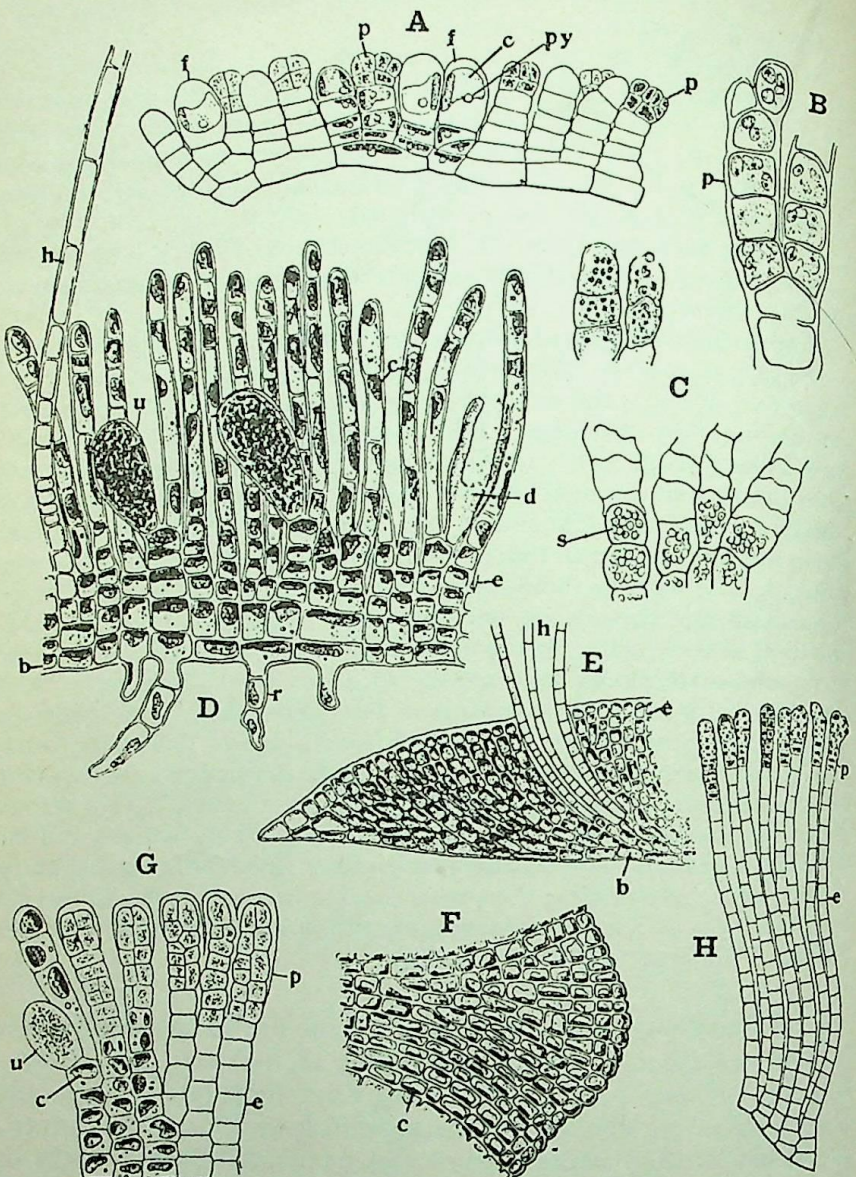

Fig. 10. Myrionemataceae. A, *Symphyocarpus strangulans* Rosenv., section of stratum. B, C, *Heribaudiella fluviatilis* (Aresch.) Sved.; B, young and C, mature plurilocular sporangia. D, F, G, *Ralfsia clavata* (Carm.) Crouan; D, section of stratum, with mature unilocular sporangia; F, part of basal stratum, from below; G, small part of stratum in vertical section, with plurilocular sporangia. E, *R. verrucosa* Aresch., vertical section of a growing thallus. H, *Petroderma maculiforme* Kuck., erect threads with plurilocular sporangia. *b*, basal stratum; *c*, chromatophore; *d*, dehisced unilocular sporangium; *e*, erect threads; *f*, fucosan-cells; *h*, hair; *p*, plurilocular and *u*, unilocular sporangium; *py*, pyrenoid; *r*, rhizoid; *s*, swarmer. (A, H after Kuckuck; B, C after Svedelius; the rest after Reinke.)

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(106) p. 103, (133) p. 244) they are arched (fig. 10 E). Long colourless hairs with a basal meristem, borne on the ends of short threads (fig. 10 D, *h*) or arising directly from the basal system, appear embedded among the fused threads; they either occur singly or appear in tufts which sometimes arise from funnel-shaped pits (fig. 10 E, *h*). The single chromatophore is usually apposed to the upper wall of the cell (fig. 10 D).

In the reproductive phase, which sets in in late autumn, the erect threads grow out over localised areas as free filaments and form a number of sori appearing as flat warts on the crusts. The unilocular sporangia (fig. 10 D, *u*) are borne laterally on the free threads, while

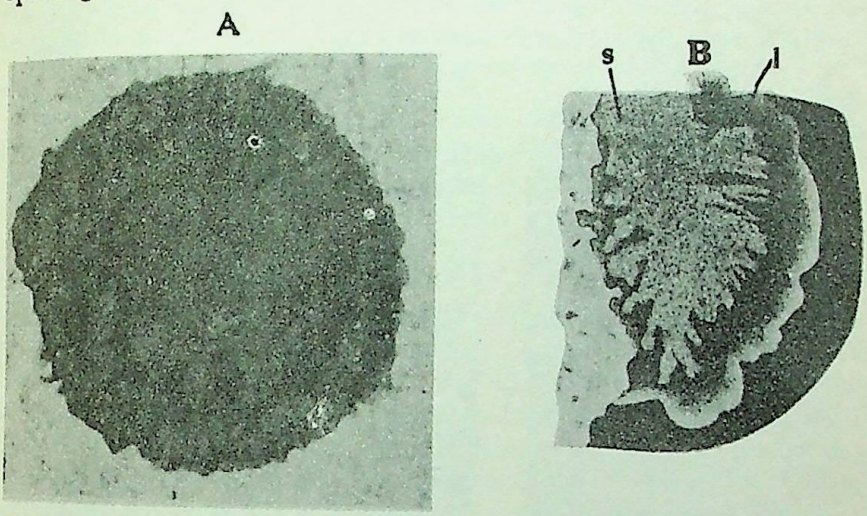

Fig. 11. A, *Ralfsia verrucosa* Aresch., old crust (photo.: P. L. Anand). B, *Lithoderma fatiscens* Kuck., old crust (*l*) with sorus (*s*) of plurilocular sporangia (after Kuckuck).

the pluriloeular ones (fig. 10 G, *p*) are terminal in position ((18) p. 286, (32) p. 191, (133) p. 241, (190) p. 140). After liberation of the swarmers the fertile threads are shed, while the parts below continue to grow ((190) p. 140). Vegetative enlargement, involving both increase in thickness and marginal growth, takes place during spring and summer. *Mesospora* ((64) p. 263, (289) p. 27) combines the lateral position of the unilocular sporangia seen in *Ralfsia* with a lack of fusion between the erect threads as in *Nemoderma* (see also (303) regarding *Hapalospongidium*).

The similar crusts formed by *Lithoderma* ((133) p. 237, (145) p. 165, (190) p. 144, (203) p. 97; fig. 11 B) are at first light-coloured; the species are characteristic of colder seas and are found more particularly in winter in the sublittoral region. The coalescence of the erect threads, even in fertile plants, is very marked (fig. 12). There is only a single sorus composed of uni- or plurilocular sporangia (fig. 11 B, *s*). The

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cells contain several chromatophores, although in those of the free threads there is generally only one; in the northern forms hairs are completely lacking (cf. (261) p. 19).

The principal species, *L. fatiscens* Aresch. (*L. extensum* (Crouan) Hamel), was described as bearing the plurilocular sporangia laterally on projecting threads ((11) p. 23, (118) p. 18, (149) p. 45). Kuckuck ((145) p. 165) subsequently found an otherwise similar form with terminal plurilocular sporangia (fig. 12 B, *p*) and suggested that Areschoug's plant was wrongly ascribed to this species. Most authorities have followed Kuckuck in regarding the sporangia as terminal, while some

Fig. 12. *Lithoderma fatiscens* Kuck. (after Kuckuck), vertical sections of two strata; A, with unilocular, B with plurilocular sporangia. *d*, dehisced unilocular sporangium; *e*, erect threads; *p*, plurilocular and *u*, unilocular sporangium; *s*, swarmer.

((256) p. 501) even describe their position as variable. Svedelius ((122) p. 176), however, regarded the two forms as distinct and referred Kuckuck's alga to a separate genus *Pseudolithoderma*. Recent investigations of Lund (165) lend considerable support for this view (cf. also (271)), and the *Lithoderma* of Kuckuck with terminal uni- and plurilocular sporangia (fig. 12), normally borne on distinct individuals, must be regarded as different from that of Areschoug with lateral plurilocular sporangia. Whether generic separation is justified remains to be seen. Lund advances considerable evidence in favour of the view that *Ralfsia ovata* Rosenv. ((202) p. 900), which is known only with lateral unilocular sporangia, may be the asexual phase of Areschoug's *Lithoderma fatiscens* (cf. also (111) p. 142, (203) p. 94).

Certain freshwater forms found in rapid-flowing streams ((73) p. 169,

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(78), (105) p. 117, (262)), formerly included in *Lithoderma* ((11) p. 24, (67), (203)), have recently (270) been again referred to Gomont's genus *Heribaudiella* ((83) p. 388). The distinctive feature lies in the plurilocular sporangia, which are constituted by five or six of the uppermost cells of an erect thread (fig. 10 B, *p*), each of which without further septation forms a number of swarmers (fig. 10 C, *s*). The large unilocular sporangia are also terminal. The vegetative cells contain a number of discoid or lobed chromatophores. Klebahn's *Lithodora* (124) is probably a *Heribaudiella*, intimately admixed with some other alga.

In *Symphyocarpus* ((23), (133) p. 236, (150) p. 17, (202) p. 896, (203) p. 67), an epiphyte in the sublittoral region, the erect filaments are short (fig. 10 A) and bear the plurilocular sporangia (*p*) terminally. There are occasional hairs, while at certain points the upright threads are replaced by large cells (*f*) full of fucosan-vesicles; these were regarded by Kuckuck as homologous with the paraphyses of *Scytosiphon*.

It is not improbable that some of the genera above discussed are reduced types, although in the present state of knowledge it is difficult to get adequate evidence for this point of view.

A more elaborate structure is found in the Elachistaceae, well exemplified by *Elachista*. Here and in the families subsequently to be considered a greater degree of anatomical specialisation exists than in the Myrionemataceae. The thalli are differentiated into a colourless, basal or central, medullary region and a peripheral photosynthetic cortex. The latter produces three kinds of structures which in the subsequent matter are distinguished as follows: (*a*) long threads of more or less indefinite growth with cells containing chromatophores, the *assimilatory hairs*; (*b*) shorter and often copiously branched threads of limited growth, the *assimilators* (paraphyses of many writers); (*c*) long threads with colourless cells, the *colourless hairs*.

Elachista[1] comprises a number of widely distributed epiphytes, which are specially common on Fucales; thus, *E. scutulata* (fig. 13 C) is found on the receptacles of *Himanthalia*, the swarmers germinating in the conceptacles from which the cushions of the epiphyte later project, while the very common *E. fucicola* Fries is chiefly found on species of *Fucus*. The mature plants form small, firm, often hemispherical cushions which are densely pilose (fig. 13 C). The lower part of the adult thallus (fig. 13 A) is constituted by a more or less extensive medulla composed of dense vertical rows of almost colourless cells (*m*), which in some species at least are firmly joined together. The upper part (cortex, *c*) is likewise often compact, although the component threads are not laterally united. They comprise more or less numerous assimilators (*a*), which are commonly curved, moniliform, and frequently clavate in shape (fig. 13 B, *a*), and, projecting

[1] Originally spelt *Elachistea*, which is etymologically incorrect. For the general literature, see (6) p. 9, (87) p. 117, (247) p. 168, (261) p. 21, (273), (280) p. 236, (281) p. 19.

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from amid them and often preponderating, the unbranched assimilatory hairs (*h*). The cells of the latter are densely filled with chromatophores, except for some of the uppermost which tend to decay early ((204) p. 19, (246) p. 146). These structures, which sometimes reach a length of a centimetre, in many species probably constitute the chief photosynthetic system. There are no colourless hairs.

Young stages of *Elachista*[1] exhibit the usual discoid basal system (fig. 13 H) of a single layer of cells ((147) p. 23, (153) p. 12, (204), (246) p. 144). From the latter arise numerous unbranched assimilatory hairs (fig. 13 I, *h*), the basal cell of which is sometimes much narrowed. These erect threads at first exhibit uniform division of their cells, but subsequently differentiate a little above the base an intercalary meristem (*i*) ((121) p. 216, (147) p. 63) which cuts off series of photosynthetic cells to the outside. A cell below the meristem sooner or later puts forth a lateral branch which develops into a secondary assimilatory hair (fig. 13 I, *h'*). This in its turn acquires a meristem and branches in the same manner, and so there appear upon the basal system a number of primary tufts which gradually close together to form a cushion. The medulla arises through enlargement of the cells that bear branches (fig. 13 G, *m*), in some species perhaps supplemented by an active formation of new cells from the overlying meristem.[2] The assimilators, like the secondary assimilatory hairs, originate from the cells below the meristem and as a rule probably only commence to develop at a later stage; ultimately they are often produced in considerable numbers (*E. fucicola*), although scanty in some species (*E. intermedia*, fig. 13 F, G; (147) p. 25), and it is not impossible that there may be some degree of variability in this respect in one and the same form.

The assimilators are no doubt homologous with the assimilatory hairs, but growth becomes arrested before the intercalary meristem is established (cf. (147) p. 25, (247) p. 169). The meristems of the diverse assimilatory hairs tend to be located at approximately the same horizontal level and lie just above the point at which the cortex commences. Characteristic of Elachistaceae are the large, pear-shaped, usually sessile unilocular sporangia (fig. 13 G, *u*), which are borne laterally on the basal parts of the assimilators and often occupy a zone a little way above the medulla (fig. 13 A, *u*). The plurilocular sporangia either form intercalary sori on the upper parts of the hairs (*E. lubrica*, fig. 13 J) or occur terminally on the assimilators (fig. 13 F).

The species of *Elachista* appear in general to be annuals ((147) p. 22, (190) p. 160, (204)), the cushions commencing to develop in the early

[1] This account of the early development is essentially based on Sauvageau's (246) study of *E. intermedia* Crouan and there are probably minor differences in other species.

[2] Kjellman ((121) p. 217) also speaks of thin, downwardly growing threads, but no other writer has recorded these.

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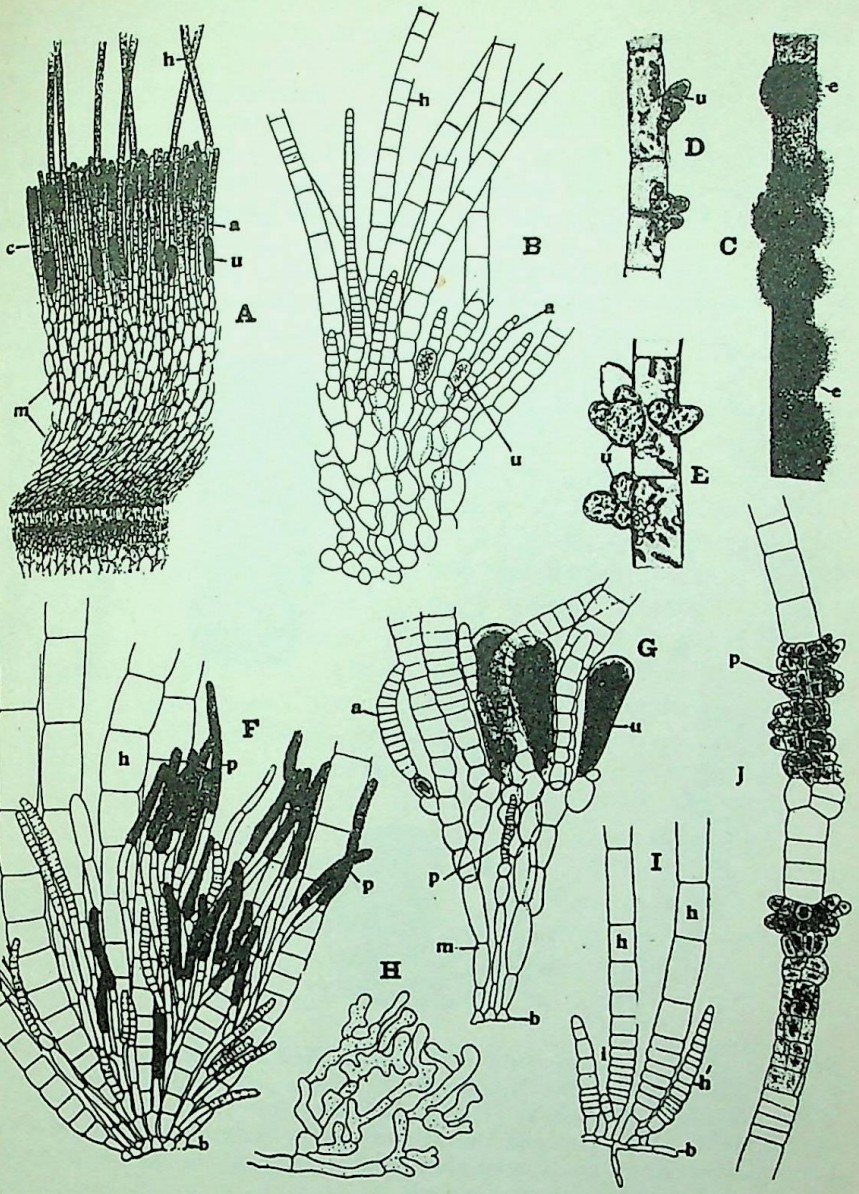

Fig. 13. *Elachista* A, C, *E. scutulata* Duby; B, D, E, *E. stellaris* Aresch.; F–I, *E. intermedia* Crouan; J, *E. lubrica* Rupr. A, B, vertical sections of strata with unilocular sporangia; C, several plants (*e*) on a receptacle of *Himanthalia*; D, E, unilocular sporangia on assimilatory hairs; F, section of a stratum with plurilocular sporangia; G, the same with both kinds of sporangia; H, part of a young basal stratum in surface view; I, early development of erect system; J, assimilatory hair, with plurilocular sporangia. *a*, assimilator; *b*, basal stratum; *c*, cortex; *h*, *h'*, assimilatory hairs; *i*, intercalary meristem; *m*, medulla; *p*, plurilocular and *u*, unilocular sporangium. (A, C after Thuret & Bornet; B, D after Rosenvinge; H, I after Sauvageau; the rest after Kuckuck.)

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spring and dying away during the winter, although sometimes fresh assimilatory hairs can apparently arise in spring from persisting parts of the thalli ((130) p. 65, (182) p. 34). Formation of reproductive organs normally begins in autumn and may continue through most of the winter; in *E. fucicola* Rosenvinge (204) records the production of unilocular sporangia in quite young plants and this is clearly not uncommon.

Symphoricoccus was established by Reinke ((197) p. 17, (198) p. 52, (199) p. 3) for an alga with the structure of an *Elachista* but bearing

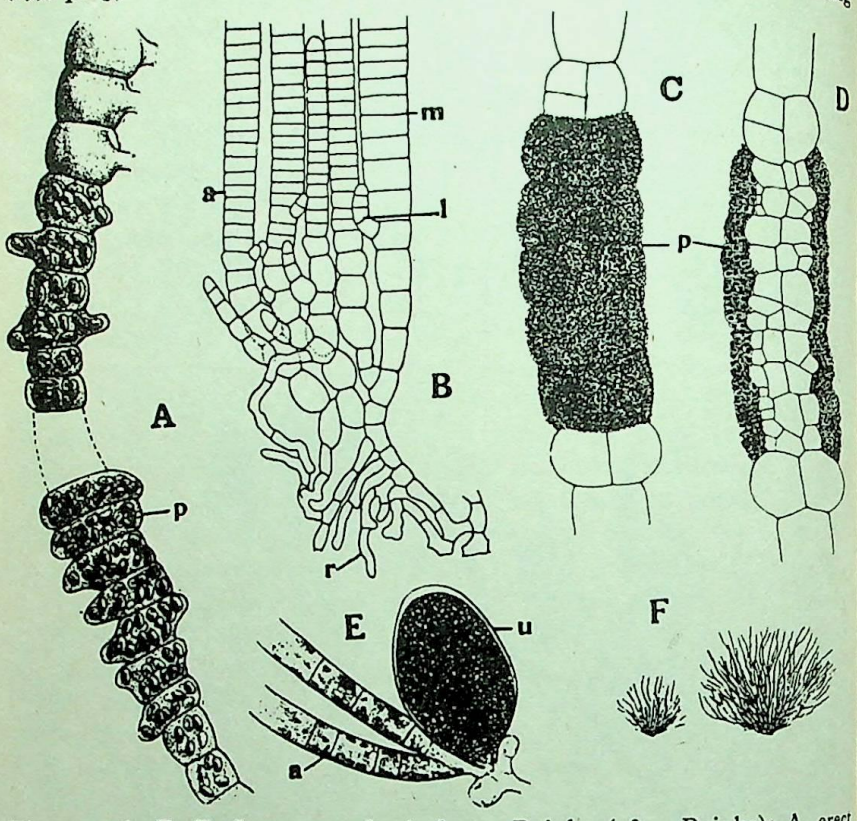

Fig. 14. A, E, F, *Leptonema fasciculatum* Reinke (after Reinke); A, erect thread with plurilocular sporangia; E, unilocular sporangium; F, habit. B–D, *Halothrix lumbricalis* (Kütz.) Reinke (after Kuckuck); B, base of a young plant; C, D, parts of assimilatory hairs, with plurilocular sporangia, in optical section in D. *a*, assimilatory hair; *l*, lateral; *m*, meristem; *p*, plurilocular and *u*, unilocular sporangium.

uni- and plurilocular sporangia laterally, both on the bases of the assimilators (fig. 13 B) and on the upper parts of the assimilatory hairs (fig. 13 D, E). To this genus Kuckuck ((147) p. 34) referred *E. stellaris* Aresch. ((84) p. 26, (149) p. 60), which shows the same features. Many authorities hold, however, that the establishment of a distinct genus is not warranted (cf. (153) p. 10, (204) p. 27, (245)).

Other members of Elachistaceae form minute epiphytic growths, which possess but an ill-defined medulla (fig. 14 B). This is so in *Leptonema fasciculatum* ((147) p. 34, (198) p. 50, (199) p. 13, (206) p. 38,

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(249) p. 174, (268) p. 94; fig. 14 F), which Hamel ((87) p. xii) refers to Ectocarpaceae; the affinity with *Elachista* is, however, shown not only by the long unbranched assimilatory hairs, but by the large pyriform unilocular sporangia that arise at their base (fig. 14 E). The plurilocular sporangia (fig. 14 A) are formed in the upper parts of the hairs. Another species of this genus, *L. lucifugum* Kuck. ((26), (134) p. 387, (137), (162) p. 47), which appears to be not uncommonly associated with *Rhodochorton Rothii* in caves (288), shows ((204) p. 40, (263)) considerable branching of the upright threads. Whether this is really one of the Elachistaceae remains to be seen. *Halothrix* ((147) p. 26, (198) p. 49, (199) p. 1, (204) p. 37, (274)) is distinguished by the fact that the sori of plurilocular sporangia (the only ones known) form dense girdles around the assimilatory hairs (fig. 14 C, D; cf. *Zosterocarpus*).

The somewhat divergent genus *Giraudya* ((55) p. 650, (82) p. 193, (147) p. 28, (231)), a rather rare sublittoral European form, is included in the Elachistaceae by most authorities (cf. however (87) p. 189, (152) p. 93). The upright threads, which form minute tufts, here develop into fusiform parenchymatous structures (fig. 15 A–C), 8–10 mm. long; these bear terminal and lateral sheathed hairs (fig. 15 E, F, *h*), with a basal growing point (*g*), which are lacking in other Elachistaceae. The assimilatory threads are widest in the region of the intercalary meristem, which is situated towards their base. According to Sauvageau ((231) p. 17) the ill-defined medulla is formed by interlacing rhizoids originating from the lower cells of the erect threads (fig. 15 G, K, *r*); these rhizoids can produce new assimilatory filaments (fig. 15 H, *a*; cf. also (82) p. 195), although the latter also originate from the basal parts of the primary threads (fig. 15 I, *l*). The medulla of *Giraudya* would thus appear to differ in origin from that of *Elachista*. The apical parts of the successive assimilatory threads gradually wear away or are used in the production of sporangia. *Giraudya*, though a polystichous form, has much in common with the Elachistaceae in its method of branching.

Only plurilocular sporangia have been observed and of these Sauvageau distinguishes three types. One kind, arising by division of the peripheral cells in the upper parts of the assimilatory threads, forms dense sori partly encircling the latter (fig. 15 A, B, D, *s*). Others (*e*), occurring in a similar position, form small excrescences on the surface, while those of the third type, which are not uncommonly branched (fig. 15 L), are clustered around the bases of the threads (fig. 15 C, M, *b*) beneath the intercalary meristem.

Gelatinous cushion-forms

A series of forms, conveniently grouped as Leathesiaceae ((256) p. 507; Corynophlaeaceae of Kuckuck[1] and Oltmanns (147) p. 35), appear

[1] Kuckuck ((147) p. 8) regards the Myrionemataceae as reduced members of this family, but for this view it is difficult to find adequate evidence.

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closely related to Elachistaceae. They are characterised by a considerably greater production of mucilage. As in *Elachista*, it is possible to distinguish a large-celled medulla (fig. 16 E, *m*) composed of

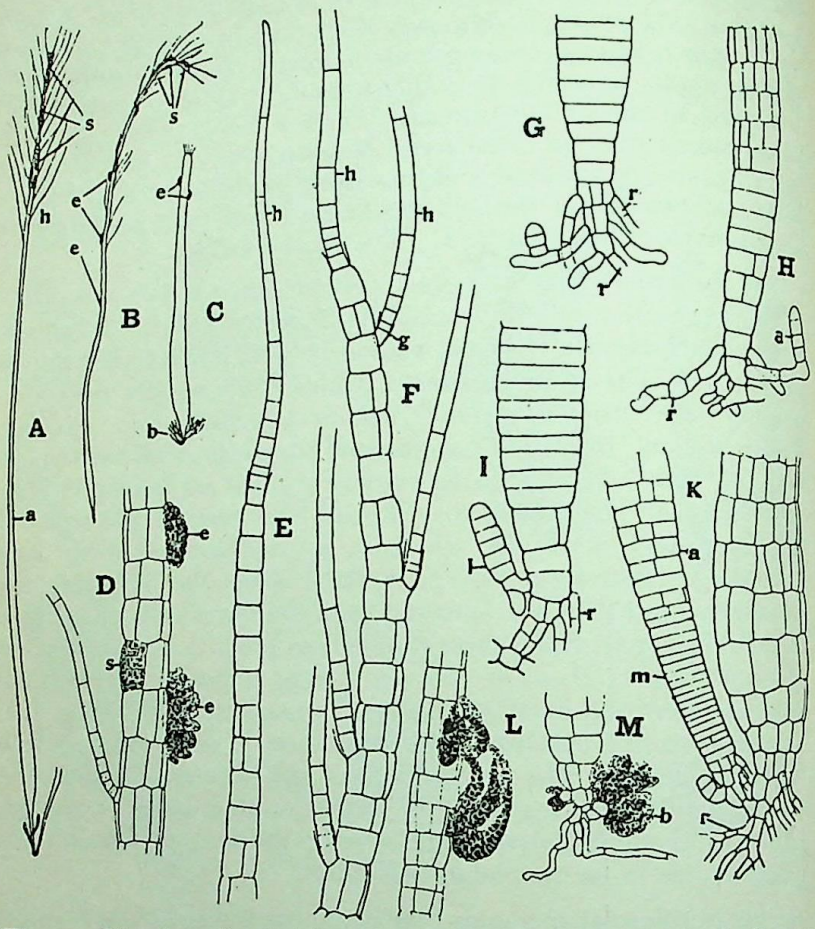

Fig. 15. *Giraudya sphacelarioides* (Derb.) Sol. (after Sauvageau). A–C, erect threads of three plants, showing the diverse disposition of the sporangia; D, upper part of a thread with embedded (*s*) and projecting (*e*) sori; E, F, apices of young and older threads respectively; G, base of thread showing rhizoid-formation; H–K, basal parts of threads showing formation of secondary assimilators; L, M, bases of threads with sori. *a*, assimilator; *b*, basal sporangia; *e*, projecting sporangia; *g*, sheath; *h*, hair; *l*, lateral; *m*, meristem; *r*, rhizoid; *s*, embedded sori.

compacted threads and a peripheral photosynthetic cortex (*a*) from which numerous colourless hairs (*h*) project. In *Myriactula* (*Myriactis*,[1] (19), (64) p. 272, (147) p. 35, (192), (246) p. 151), which is

[1] The name *Myriactis*, having previously been given to a Composite genus, must be abandoned. The use of the name *Gonodia* (176) for this genus is in no way justified (cf. (246) p. 152).

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commonly ((130), (150) p. 13, (256) p. 507) placed among Elachistaceae and most of the species of which were originally assigned to *Elachista*, the chief distinctive feature is indeed constituted by these colourless hairs which replace the assimilatory hairs of the latter genus. The facts suggest that the two types of structures are homologous (cf. (247) p. 167).

Myriactula pulvinata ((281) p. 18), not uncommonly epiphytic on Fucales (*Cystoseira*, fig. 16 A, *p*; *Halidrys*), forms small gelatinous cushions, the lower part of which is completely embedded in the conceptacles (fig. 16 E). The cortex consists of numerous assimilators (*a*) which taper at each end (fig. 16 C, D, *a*) and bear the hairs (*h*) laterally. The early development appears to be much as in *Elachista*. In *M. stellulata* (*Elachista stellulata* Griff. (147), (207)), a rare endophyte in *Dictyota dichotoma* (fig. 16 B), creeping threads (*c*) extend horizontally beneath the superficial cells of the host and function as stolons from which a series of cushions can arise. The medullary threads penetrate the surface-layer of the host, which is always wanting at the place where a cushion occurs (fig. 16 B). In *Myriactula* both kinds of sporangia ((280) p. 237) are borne as lateral outgrowths at the base of the assimilators (fig. 16 B–E).

In this genus, as in *Elachista*, medulla and cortex are as a general rule of approximately equal size, but in *Leathesia* ((113), (147) p. 43) and related genera there is an exceptionally large medulla. *L. difformis* (fig. 17 C) is an abundant annual on north temperate coasts, forming brown, rounded or lobed, gelatinous growths, up to 5 cm. in diameter, conspicuous between tide levels during summer on all kinds of substrata (rocks, other Algae). *Corynophlaea* ((6) p. 20; (147) p. 40), with a number of rarer species (incl. *L. crispa* Harv. (50)), exhibits only trifling differences (mainly the wider cortex, fig. 17 A), and it is often ((247) p. 159, (256) p. 510) merged in *Leathesia*. The prostrate base in these genera is a more or less continuous expanse (fig. 17 E) and is as usual older than the erect-growing portion. In the mature thallus the branching threads composing the cushion consist for the most part of large cells with few or no chromatophores (fig. 17 B, *m*) and widely separated by mucilage (*g*). This extensive medulla is covered by a narrow cortex (*c*) composed of short assimilators, the cells of which are packed with chromatophores; in *Leathesia* proper each thread consists of only 2–4 cells, the end one being enlarged (fig. 17 F, *a*). From amid the cortical threads hairs (*h*) project in considerable numbers.

The development of the common *Leathesia* has not been fully studied, but from what is known of it ((113) p. 89) and allied species ((152) p. 65, (247) p. 166) it would appear that the prostrate system first gives rise to upright threads composed of small cells (fig. 17 D, *e*); these grow by division of the basal cells and multiply by branching ((81) p. 428). The medulla is formed secondarily by progressive

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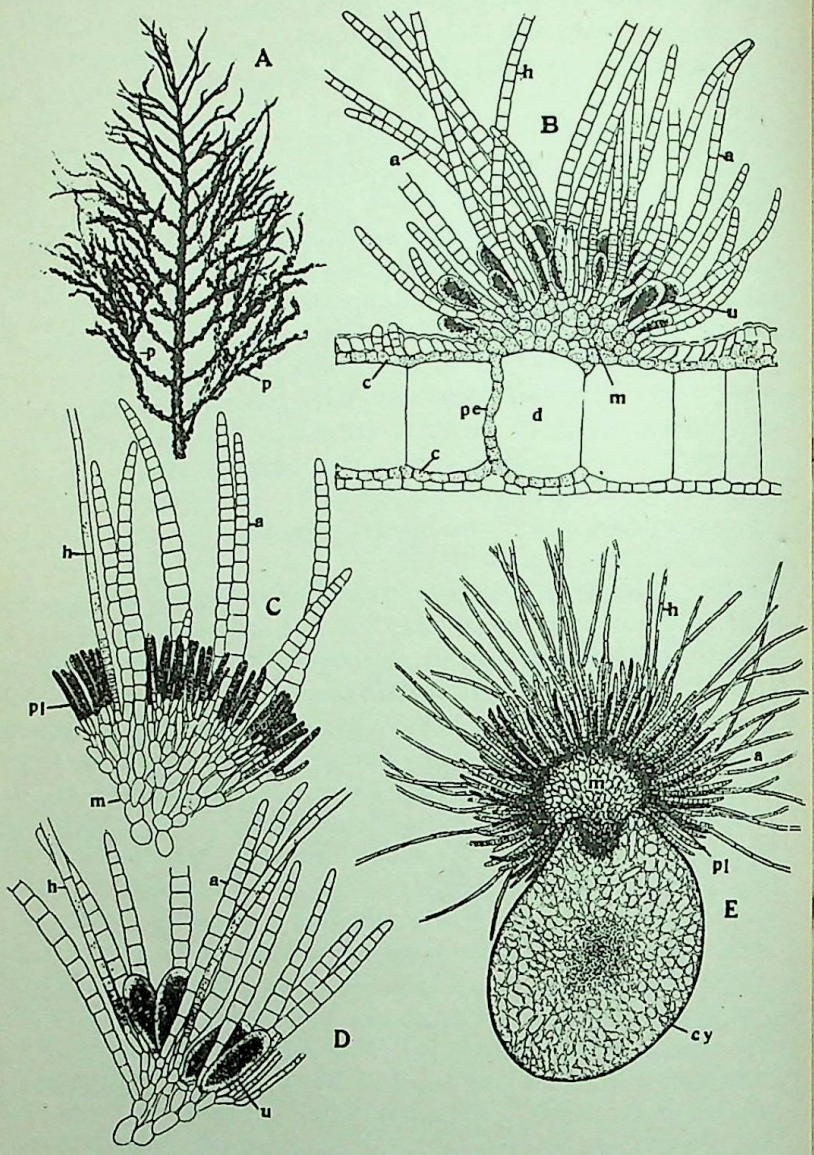

Fig. 16. *Myriactula*. B, *M. stellulata* (Griff.) Batt., the others *M. pulvinata* Kütz. A, plants (*p*) epiphytic on *Cystoseira granulata* Ag.; B, section of a cushion on *Dictyota* (*d*); C, D, tufts with plurilocular and unilocular sporangia respectively; E, transverse section of axis of *Cystoseira* (*cy*) passing vertically through a cushion of the epiphyte. *a*, assimilator; *c*, creeping endophytic threads; *h*, hair; *m*, medulla; *pe*, penetrating thread; *pl*, plurilocular and *u*, unilocular sporangium. (A, E after Thuret & Bornet; the rest after Kuckuck.)

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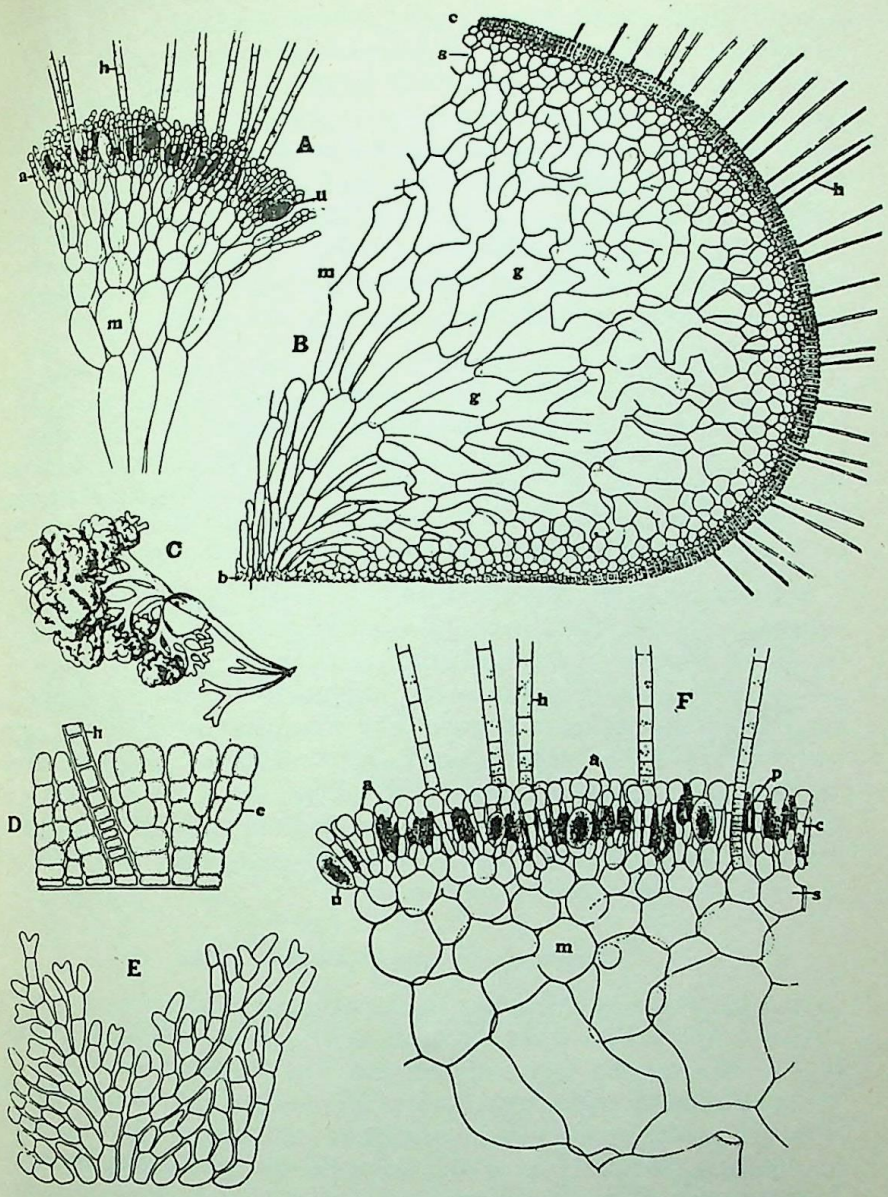

Fig. 17. A, *Corynophlaea umbellata* J. Ag., part of a cushion. B–F, *Leathesia difformis* Aresch.; B, section of half a mature cushion; C, a number of plants epiphytic on *Chondrus crispus*; D, vertical section of a young plant; E, marginal part of basal stratum of young plant; F, section through periphery of mature plant, with the two kinds of sporangia. *a*, assimilator; *b*, basal stratum; *c*, cortex; *e*, erect threads; *g*, mucilaginous wall; *h*, hair; *m*, medulla; *p*, plurilocular and *u*, unilocular sporangium; *s*, subcortex. (C after Taylor; D, E after Kylin; the rest after Kuckuck.)

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enlargement of the lower cells of the threads and is gradually intercalated between those first formed and the basal stratum. Between medulla and cortex there is an intermediate region (fig. 17 B, F, s) in which the cells are still relatively small. In *L. difformis* the older cells of the medulla assume an irregular stellate form (fig. 17 B) and exhibit a considerable number of anastomoses ((147) p. 44), so that the medulla constitutes a framework of considerable stability, the wide meshes of which are occupied by mucilage. The older thalli are commonly hollow, a condition which is more rarely realised in *Corynophlaea*. The two kinds of sporangia arise from the basal cells of the assimilators or from the perimedullary cells (fig. 17 F).

Another member of this family is *Cylindrocarpus* ((54); *Petrospongium* Naeg.) in which the medullary threads are bound together by hyphae. The plurilocular sporangia have been described by Hanna (88) in *C. Berkleyi* (Grev.) Crouan (*Petrospongium Berkleyi* Naeg.; *Leathesia Berkleyi* Harv. (95) pl. 176). *C. microscopicus* Crouan (*Ectocarpus investiens* Hauck), which is sometimes endophytic in *Gracilaria*, has been fully studied by Kuckuck ((142); cf. also (64) p. 285).

Myrionemataceae, Elachistaceae, and Leathesiaceae constitute a progressive series (though not necessarily an evolutionary one) with increasing anatomical differentiation, in all the members of which the thallus is composed of numerous equivalent upgrowing filaments emerging from the basal system. The Elachistaceae show the commencement and the Leathesiaceae the further elaboration of a proximal medulla and a distal photosynthetic cortex, the latter consisting of the ultimate branches of the threads forming the medulla. These types are therefore multiaxial. *Leathesia* can in some ways be compared with *Codium Bursa* among Siphonales.

Cylindrical uni- and multiaxial Types

In another series of gelatinous forms with essentially the same construction, the thallus takes the form of branched cylindrical strands (fig. 18) of a varying degree of firmness. The principal members may be grouped as Mesogloeaceae ((147) p. 46, (187)), which comprise such common genera as *Castagnea*, *Mesogloea*, and *Chordaria*. Kuckuck ((147) p. 8) regards the Mesogloeaceae as the direct descendants of the Leathesiaceae, while Kjellman's ((121) p. 221) Chordariaceae included not only both of these, but also the Myrionemataceae.

The radially symmetrical thallus of the Mesogloeaceae commonly exhibits differentiation into a central large-celled medulla (figs. 20 C; 22 D, *m*), a peripheral small-celled cortex (*c*), and an intervening subcortex with cells of intermediate size. Longitudinal sections of the mature thalli nearly always display a multiaxial structure (cf. fig. 22 F). The axial threads form the more or less compact medulla, while their numerous offstanding branches, which are not united,

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give rise in their inner parts to the subcortex and in their outer parts to the cortex; the latter consists largely of assimilators (fig. 21 D, *a*), between which there usually arise hairs (*h*) of the customary type.

The axial threads originate from the first-formed prostrate system (fig. 20 B, *b*) and, as a rule, several threads arising from the latter form the basis of the medulla. In *Mesogloea* and *Myriocladia*, however, there is only one such axial filament (fig. 19 A, *m*; B, *af*), the primary laterals (*l*) of which for a time run parallel to the parent-thread and thus, together with it, constitute the axial strand composing the medulla; the axial thread is usually clearly recognisable

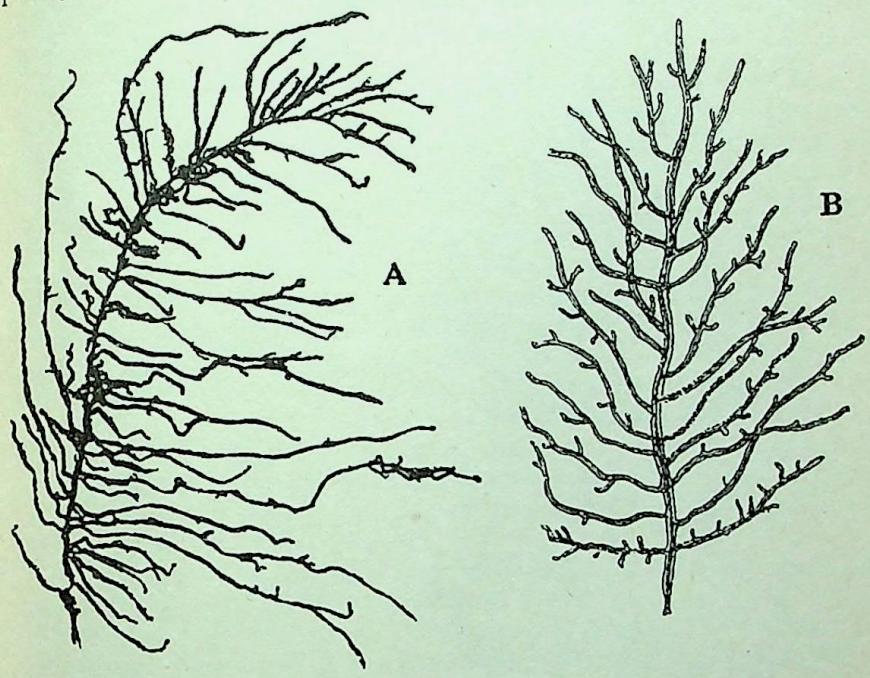

Fig. 18. A, *Mesogloea vermiculata* Le Jol. (photo.: R. Cullen). B, *Castagnea virescens* (Carm.) Thur. (after Newton).

in the apices of the thallus branches (fig. 19 A). The contrast between the basic construction of *Castagnea* and *Mesogloea*, which in other respects show considerable resemblances, is found also in other heterotrichous groups (cf. p. 445), where likewise in related types the erect fronds may in the one be derived from a single thread, in the other from a number of upgrowing threads.

Mesogloea vermiculata Le Jol. (*M. vermicularis* Ag. (95) pl. 31) (fig. 18 A) is a frequent annual near low-water mark, often attached to rocks with a thin covering of sand, though sometimes epiphytic. The more cartilaginous *M. Leveillei* ((23), (147) p. 54, (187) p. 27), sometimes placed in a distinct genus *Liebmannia* ((5) p. 60, (87) p. 166, (155) p. 7), is commoner in warmer seas. The single axial thread

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(fig. 19 A, *m*) is crowned by an assimilator (*a*) of some length, at the base of which lies a well-marked meristem (*g*). Below the latter the cells rapidly enlarge and produce primary laterals (*l*), which grow apposed to the axial thread for a considerable distance before bending outwards to terminate in a curved assimilator (*a*) like that at the apex

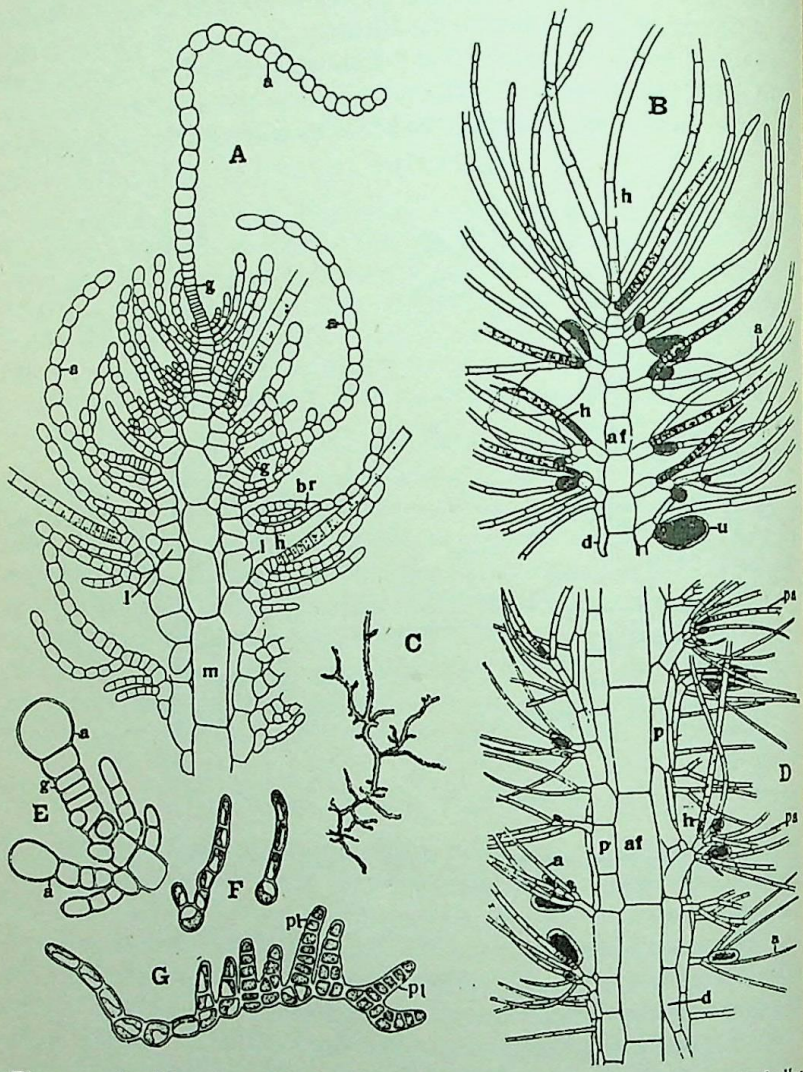

Fig. 19. A, *Mesogloea Leveillei* (J. Ag.) Menegh., apical part of thallus; B–D, *Myriocladia Lovenii* J. Ag.; B, apex of thallus; C, habit; D, older part in longitudinal section. E, *Sphaerotrichia divaricata* (Ag.) Kyl., apex of thallus. F, G, *Mesogloea vermiculata* Le Jol.; F, germlings from swarmers of unilocular sporangia; G, gametophyte. *a*, assimilator; *af*, axillary filament; *br*, branch; *d*, descending thread; *g*, meristem; *h*, hair; *l*, lateral; *m*, axial thread; *p*, perimedullary threads; *pa*, primary assimilators; *pl*, gametangium; *u*, unilocular sporangium. (A, D after Kuckuck; B after Parke; C after Newton; E–G after Kylin.)

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of the axial thread. From the part of the primary lateral below this assimilator arise secondary laterals (*br*), which form a large part of the cortex; they are usually well branched and bear lateral hairs (*h*). According to Kylin ((152) p. 52, (155) p. 6) the cells of the axial thread retain some capacity for division, the resulting segments producing further primary laterals which push their way between the others or give rise directly to hairs. In the mature thalli the axial filament is indistinguishable from the investing threads; this multiaxial central region may become fistular in the older parts. Hyphae arise from various cells of the thallus (fig. 21 D, *hy*), but they do not play so important a rôle as in *Castagnea*, although, according to Parke ((187) p. 24), they aid in producing a compact cortex.

Myriocladia, referred by Kuckuck ((147) p. 63) to a distinct family, is rightly brought by Kylin ((155) p. 7) into close association with *Mesogloea*. *Myriocladia Lovenii* J. Ag. ((5) p. 52, (6) p. 16, (147) p. 62, (149) p. 88, (152) p. 52, (155) p. 7, (160) p. 60, (187) p. 32), a rare little-branched epiphyte on *Laminaria* (fig. 19 C), possesses a single large-celled axial thread (fig. 19 B, D, *af*), enveloped by a layer of large cells again formed by close apposition of the lower parts of the whorled primary laterals (*p*); the cells in question bear tufts of elongate, little-branched assimilators (*a*), only the bases of which are embedded in the general mucilage. The apex of the primary lateral ultimately bends out and terminates in a similar tuft (*pa*) which also includes hairs (*h*). The basal cells of the primary laterals further give rise to downwardly growing threads (fig. 19 D, *d*), which produce secondary assimilators. The subapical meristem ceases to function at an early stage, but there is long-continued intercalary division extending into the region from which laterals are produced.

Certain species of *Castagnea* are commonly referred to a separate genus *Eudesme* ((6) p. 29, (121) p. 226, (147) p. 46, (149) p. 85, (187)), although this is by no means a universal practice (cf. (87) p. 157). In *Eudesme* the axial threads are readily separated by pressure under a cover-glass, whereas in *Castagnea* proper they are united into a firm parenchymatous strand a short distance behind the apex. There are also other slight differences ((187) p. 10), but, although segregation is possibly a matter of taxonomic convenience, there are no marked distinctions between the two genera and in the following account all the species are included under *Castagnea*. Setchell and Gardner ((256) p. 544; cf. also (279) p. 140) refer the species of *Eudesme* and *Castagnea* to Fries' genus *Aegira*, which has been ignored by most recent authorities owing to its inadequate basis (cf. (103) p. 505, (152) p. 57, (187) p. 21). Kylin ((155) p. 26), on the other hand, adopts the generic name *Cladosiphon* (Kützing) for the species of *Castagnea* proper.

Castagnea virescens (Carm.) Thur. (*Mesogloea virescens* Carm. (95) pl. 82, (187) p. 15, (198) p. 76, (258) p. 11) (fig. 18 B), a not uncommon annual found usually in the lower part of the littoral region, has a plentifully branched thallus which is densely villous owing to the

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numerous hairs. Another species, *C. Zosterae* ((149) p. 85), mostly epiphytic on *Zostera*, is smaller and less branched (fig. 20 A). Both of these are usually placed in *Eudesme*. The species of *Castagnea* proper are rarer in northern waters, although not uncommon in warmer seas like the Mediterranean. *C. contorta* Thur.[1] is known from British and French shores.

Sauvageau (233) has given a detailed account of the early development of *C. Zosterae*. Many of the filaments, which arise from the centre of the basal disc (fig. 20 D), are at first moniliform and devoid of terminal hairs (fig. 20 E, *pa*), so that they closely resemble the cortical assimilators of the mature thallus; subsequently the cells divide copiously and form an elongate medullary thread (fig. 20 H, K, *pf*). The basal disc, however, also bears (fig. 20 E, I) occasional sheathed hairs (*sh*) with a basal meristem, the lowest cell of which later likewise divides to form a medullary thread (*me*) which then bears a terminal hair (*ht*) devoid of a sheath; the sheaths at the base may persist (fig. 20 I, *sh*) or vanish.

The lower cells of the upgrowing threads elongate and remain narrow (fig. 20 B, *e*), but produce no laterals (cf. also (187) p. 19). Intercalary division (fig. 20 F, H, K), on the other hand, takes place in most of the upper cells and is accompanied by the outgrowth of numerous assimilators (fig. 20 E–G, *a*) and of occasional sheathed lateral hairs (*hl*). The rapid growth of these hairs often results in displacement of the distal portion of the primary filament so that the hair appears terminal (fig. 20 B, *h*).[2] Growth is then carried on by division of the cell beneath the hair and leads to the production of further laterals, one or other of which may assume the terminal position ((155) p. 23, (233) p. 403), thus leading to a sympodial construction. Diverse other investigators have arrived at the conclusion that the development of the primary filaments in *Castagnea* takes place sympodially ((32) p. 185, (152) p. 56, (187) p. 22; cf. also (147) p. 48), the axial threads being built up of the successive basal portions of laterals (fig. 21 B, *1–3*), the apical parts of which are deflected to form the subcortex and cortex.[3] This is in contrast to most Mesogloeaceae, in which the axial threads branch monopodially.

[1] According to Kylin ((155) p. 26) the *C. contorta* described by Parke ((187) p. 18) is *C. fistulosa* Derb. et Sol. (*Cladosiphon mediterraneus* Kütz.).

[2] According to Parke ((187) p. 16; cf. also (32) p. 185) all the primary filaments, in the species examined by her (incl. *C. Zosterae*), terminate in sheathed hairs (cf. fig. 21 C), but in view of Sauvageau's observations it appears probable that the terminal position is secondary (cf. also (155) p. 26).

[3] Among the immediate allies of *Castagnea* there are evidently certain differences in the way in which this sympodial growth is accomplished. Examples are the Australian *Bactrophora* (cf. (6) p. 22, (282), (290) p. 139) and Sauvageau's *Gontrania* ((246) p. 186), both of which are included by Kylin in *Castagnea* (*Cladosiphon*).

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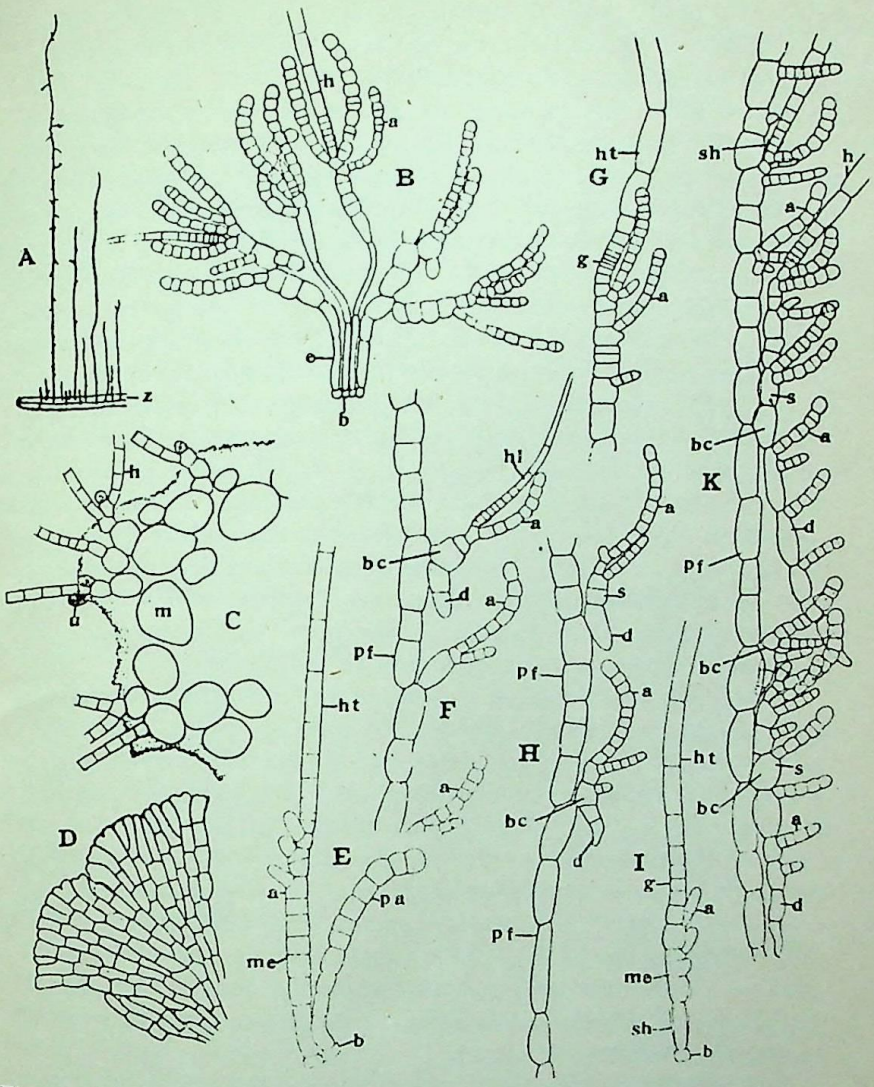

Fig. 20. *Castagnea Zosterae* Thur. (after Sauvageau). A, plants of different ages on leaf of *Zostera* (*z*). B, development of erect threads from basal system. C, section of mature thallus, with young unilocular sporangia. D, basal stratum from the surface. E, G, I, development of assimilators. F, H, development of descending filaments (*d*). K, later development of a primary erect filament. F and G are parts of same filament. *a*, assimilator; *b*, basal system; *bc*, basal cell of assimilator; *d*, descending filament; *e*, erect thread; *g*, meristem of hair; *h*, hair; *hl*, lateral hair; *ht*, terminal hair; *m*, medulla; *me*, medullary thread; *pa*, primary assimilator; *pf*, primary filament; *s*, erected part of lateral; *sh*, sheath of hair; *u*, unilocular sporangium.

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The cells of the first-formed axial filaments of *Castagnea* thus come to bear numerous well-branched laterals, but this primary condition is complicated by considerable secondary activity leading to a more compact structure. Supplementary medullary threads, bearing numerous secondary laterals, are produced by the development of downwardly growing threads (fig. 20 F, H, *d*) from the basal cells of some of the primary laterals. In *C. Zosterae* and *C. fistulosa* ((187) p. 20) they constitute a large-celled perimedullary envelope (cf. figs. 20 K, *d*; 21 A) and can scarcely be distinguished from the original axial threads except by their mode of origin. Their numerous laterals (*a*) push in between the primary ones and contribute a further system of assimilators to the cortex; the basal cells of these secondary assimilators sometimes repeat the same process. According to Parke ((187) p. 17) such downgrowing threads are not produced in *C. virescens*.

Perimedullary threads also appear to originate by the erection of certain primary laterals (fig. 20 K, *s*) which grow parallel to the original axial threads for a considerable distance (cf. *Mesogloea*) and contribute other secondary assimilators to the cortex. According to Sauvageau ((233) p. 407) this is due to intercalary division of the basal cells of the primary lateral. Branching hyphae, which are probably largely mechanical in function, may grow out from any cell. In *C. fistulosa* they form an investment to the medulla.

In the mature thalli of *Castagnea* the medullary threads often separate, leaving a cavity occupied by gas (fig. 20 C). The inner cells of the laterals forming the cortex and subcortex commonly elongate appreciably, while the smaller outer ones bear copious branches, but in many species (e.g. *C. virescens*) there is no very sharp boundary between the two regions. On the other hand, in *C. crassa* (*Mesogloea crassa* Suring. (266) p. 85), which Kylin ((155) p. 33) makes the type of a separate genus (*Tinocladia*), cortex and subcortex are sharply differentiated (fig. 21 E). The ultimate laterals, the assimilators, are usually moniliform and not uncommonly curved (fig. 21 B, *a*). Branching of the thallus is effected by the outgrowth of series of medullary filaments.

Castagnea and *Mesogloea*, which thus differ appreciably in their basic construction, probably represent divergent developments from a common source. In both the primary threads and their laterals normally terminate in assimilators, and the development of the medulla in *Mesogloea* by erection of laterals is repeated in *Castagnea* on the part of each individual primary filament. The early development of the thallus in *C. Zosterae* shows similarities to that of *Leathesia* (p. 73). In both assimilators are first produced, while the medulla originates secondarily.

The cartilaginous thalli of *Chordaria* ((6) p. 62, (63) p. 9, (99), (147) p. 60, (155) p. 39, (198) p. 74, (200) p. 57) show a more compact structure. In *C. flagelliformis* ((95) pl. 111), a frequent annual between tide-marks,

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the elongate main axis bears whip-like branches which exhibit little further branching (fig. 22 A); the entire surface is clothed with long hairs (fig. 22 D, *h*) with very gelatinous membranes. Transverse

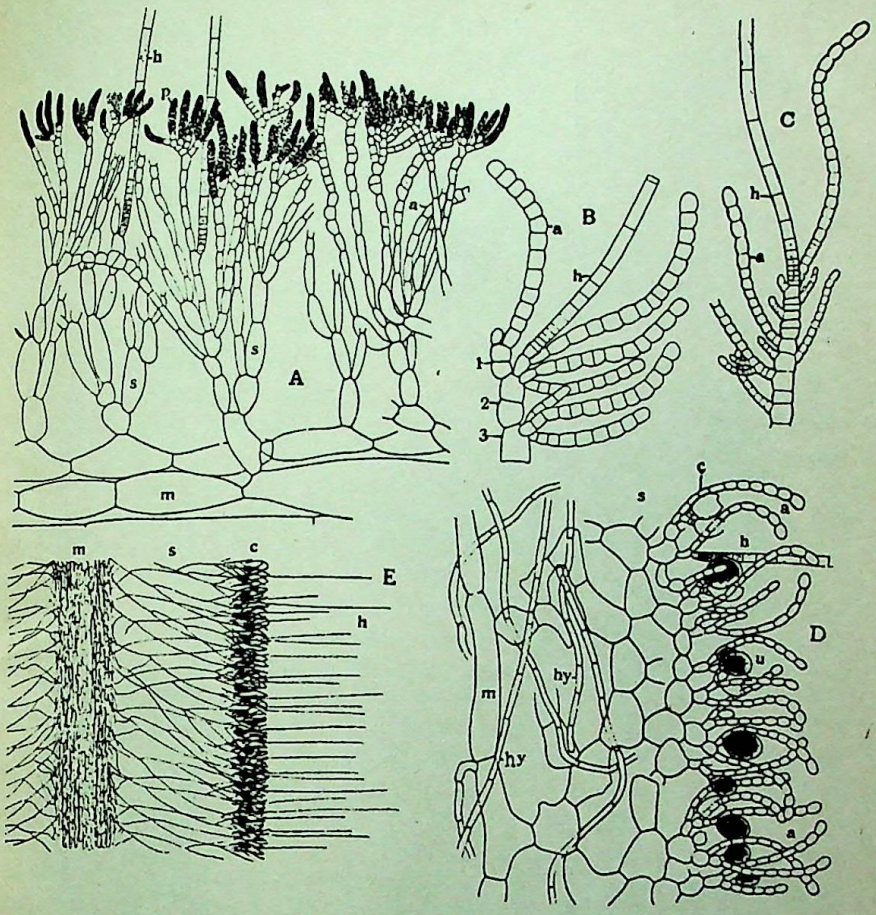

Fig. 21. A, *Castagnea contorta* Thur., periphery of thallus in longitudinal section, with plurilocular sporangia. B, *C. fistulosa* Derb. & Sol., apex of an axial thread, showing sympodial growth, *1–3* successive segments of the sympodium. C, *C. virescens* (Carm.) Thur., apex of medullary filament. D, *Mesogloea vermiculata* Le Jol., peripheral part of thallus in longitudinal section, with unilocular sporangia. E, *Castagnea crassa* (Sur.) Kuck., longitudinal section of part of thallus. *a*, assimilator; *c*, cortex; *h*, hair; *hy*, hyphae; *m*, medulla; *p*, plurilocular and *u*, unilocular sporangium; *s*, subcortex. (B after Kylin; C after Parke; the rest after Kuckuck.)

sections of the thallus show a broad, compact medulla (fig. 22 D, *m*) and a narrow cortex (*c*); the cells are smaller than in other members of this family. The medulla consists of larger (primary) cells (*mf*) intermingled with numerous narrow hyphae (*hy*); the latter are outgrowths from the medullary cells and grow vertically upwards and

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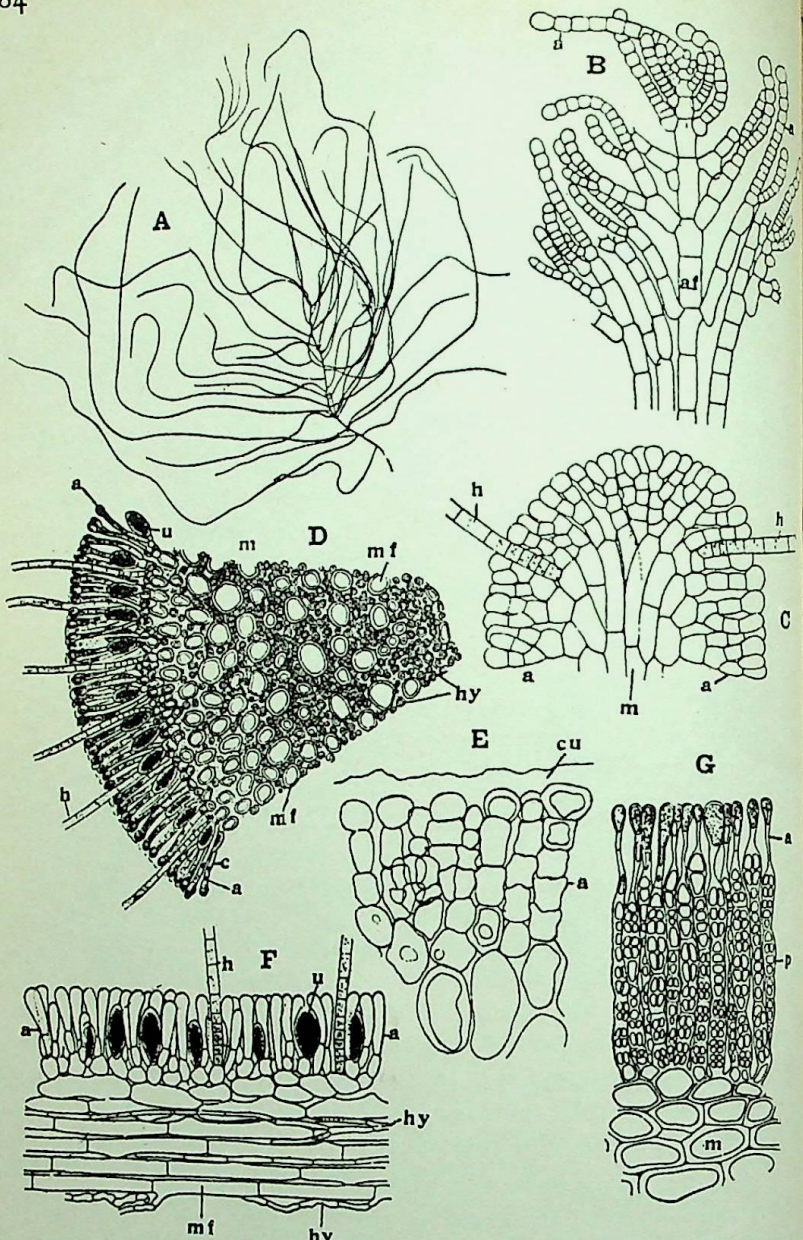

Fig. 22. A, C–F, *Chordaria*; A, D, E, *C. flagelliformis* (Müll.) Ag.; C, F *C. Chordaria* (Harv.) Kuck. A, habit; C, apex of thallus; D, transvers section of same; E, peripheral part enlarged; F, longitudinal section of pa of thallus, with unilocular sporangia. B, *Haplogloea Kuckuckii* Kyl., apex thallus. G, *Heterochordaria abietina* (Rupr.) Setch., section, with plurilocul sporangia. *a*, assimilator; *af*, axial filament; *c*, cortex; *cu*, cuticle; *h*, hai *hy*, hypha; *m*, medulla; *mf*, medullary filament; *p*, plurilocular and *u*, un locular sporangium. (A, photo.: R. Cullen; D after Reinke; E after Hencke G after Setchell & Gardner; the rest after Kuckuck.)

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downwards (fig. 22 F, *hy*). There is no subcortex, the comparatively short and well-branched assimilators (fig. 22 D, F, *a*) arising directly from the medullary threads; the branches of the assimilators are produced abaxially (fig. 22 C, *a*) and combine to form a dense layer from amid which the hairs (*h*) project.

The end-cells of the assimilators and of their branches are often enlarged and provided with a strongly thickened outer wall (fig. 22 D, E, *a*); in the Australian *C. Chordaria* ((147) p. 61) the assimilators consist of only two cells, of which the outer is elongate (fig. 22 F). In the growing tips there are a number of axial threads (fig. 22 C), each with an ill-defined meristematic region at the base of the apical assimilator; their laterals, terminating in branched assimilators, apparently insert themselves continuously between those already present, giving the apices a fan-like appearance. The branching of the axial threads is monopodial, as in *Mesogloea*.

Numerous variants on the types of construction above considered are found among Mesogloeaceae. A number of genera lack the colourless hairs found in other members of the family. Thus, in the highly mucilaginous *Myriogloea Sciurus* ((147) p. 62, (161), (187) p. 29; *Myriocladia Sciurus* Harv. (6) p. 19, (93) pl. 58), which is not uncommon in the Southern Hemisphere and has much the habit of a *Castagnea*, the multiaxial medulla is encased in a dense cortex composed of long unbranched assimilatory hairs (cf. also (66)). Each of the medullary threads possesses a sharply defined intercalary meristem (fig. 24 D, *g*), surmounted by one of these hairs and, as the axial threads increase in number by branching (*br*) below the meristem, the outermost ones diverge in a fan-like manner. There is resemblance to *Elachista* in the presence of assimilatory hairs and in the relation of the different parts to one another. The medullary threads give rise to branched hyphae which run horizontally between the former. According to Parke ((187) p. 29) the sporangia arise laterally at the level of the intercalary meristem and the two kinds occur on distinct plants. Kylin ((155) p. 12), however, states that *M. Sciurus* lacks plurilocular sporangia, while those of other species are formed in the upper parts of the assimilatory hairs. The southern types, with plurilocular sporangia originating near the bases of the assimilatory hairs, are placed (p. 15) in the new genus *Levringia*.

The American *Mesogloea Andersonii* Farl. ((63) p. 9), which was included by Kuckuck ((147) p. 63; cf. also (256) p. 556) in *Myriogloea*, is primarily uniaxial (cf. fig. 22 B) and possesses numerous short curved assimilators amid which the sporangia arise. Levring ((161) p. 48; cf. also (155) p. 21) refers it to a distinct genus *Haplogloea*. Another uniaxial form, commonly listed as *Mesogloea divaricata* (Ag.) Kütz. or *Chordaria divaricata* Ag. (cf. (130), (163), (174*a*) p. 146, (200) p. 57), which is common on the Atlantic coasts of the United States, is according to Kylin ((155) p. 38) distinguished by the fact that cell-division is confined to the intercalary meristem (fig. 19 E, *g*) situated beneath the 2–4-celled assimilator (*a*) that caps the axial thread. Kuckuck ((147) p. 10) referred this alga to *Nemacystus* (p. 90), because he believed it grew by an

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apical cell (cf. also (200) p. 57). Kylin makes it the type of a distinct genus *Sphaerotrichia*.

Certain other, rather imperfectly known, genera show resemblances to *Chordaria*. *Heterochordaria abietina* (Rupr.) Setch. & Gardn. ((254) p. 6, (256) p. 550; *Chordaria abietina* Rupr.), a small Pacific form with numerous short branches giving the plant a fir-like habit, differs considerably from the true species of *Chordaria* ((147) p. 60) and seems to

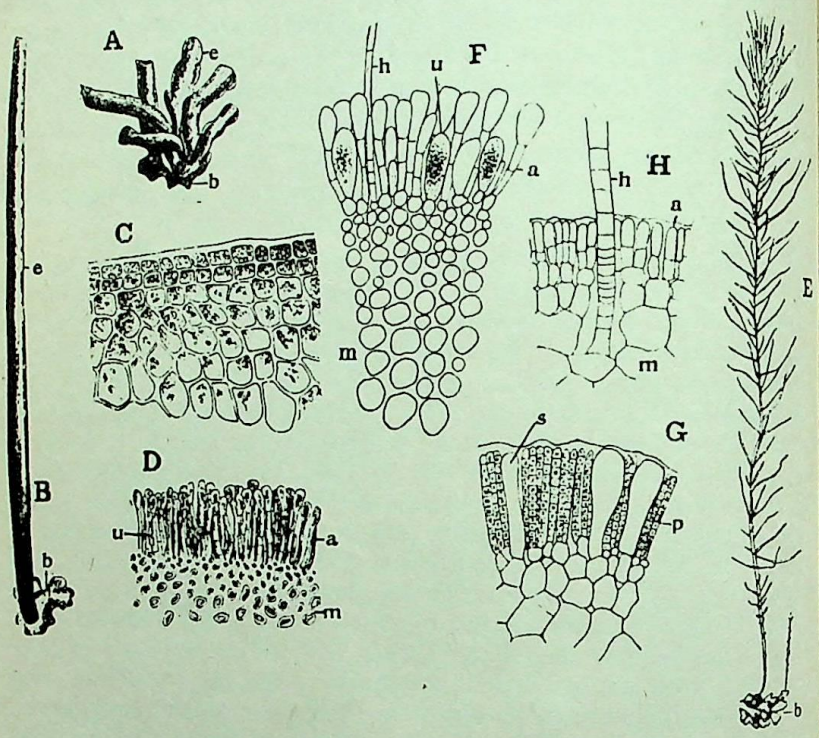

Fig. 23. A–D, *Analipus fusiformis* Kjellm.; A, B, habit; C, vertical section of basal stratum; D, peripheral part of transverse section of erect thallus, with unilocular sporangia. E–H, *Caepidium antarcticum* J. Ag.; E, habit; F, part of erect thallus, and G, of basal vesicular growth, in transverse section, with unilocular and plurilocular sporangia respectively; H, section of basal vesicular growth, with hair. *a*, assimilator; *b*, basal stratum; *e*, erect thallus; *h*, hair; *m*, medulla; *p*, plurilocular and *u*, unilocular sporangium; *s*, sterile cell. (A–D after Kjellman; E–G after Skottsberg.)

possess an isomorphic life-cycle (p. 130); it forms extensive communities below low-tide level ((76) p. 34). Both in the general habit and in the possession of a well-developed, probably perennial, basal stratum there is resemblance to the Antarctic *Caepidium* ((6) p. 58, (257) p. 40, (261) p. 27). The erect multiaxial fronds of the latter (fig. 23 E), which here arise from cup-like depressions in the lobed basal crust (*b*) and attain a height of 16 cm., have a cortex composed of usually 3-celled assimilators (fig. 23 F, *a*), with unilocular sporangia (*u*) embedded

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between them. The striking feature is the production from the basal crust at all times of the year of vesicular growths of diverse size, resembling those of *Leathesia* (p. 73). At first these develop as small solid warts showing the same structure as the ordinary erect fronds, but later they enlarge and become hollow; they bear single hairs lodged in a deep pit (fig. 23 H, *h*). These vesicles bear the plurilocular sporangia, which are formed in large irregular sori (fig. 23 G, *p*) and sometimes cover nearly the whole surface; interspersed between them are large cells (*s*) filled with dark-brown contents (fucosan?). Cotton ((53) p. 168) suggested that two distinct Algae might be involved, but Skottsberg's (261) reinvestigation leaves little doubt that the vesicles belong to the same alga as the erect fronds (cf. also (232) p. 334). In view of the probable close affinity between Mesogloeaceae and Leathesiaceae there is nothing very surprising in the erect growths from the basal stratum repeating the structural characteristics of the two families. The Pacific *Hapterophycus* (301), in which the perennial crusts produce upright branches bearing unilocular sporangia, may also belong to this affinity.

Another debatable genus is *Analipus* ((116) p. 48, (252) p. 252, (256) p. 575, (296) p. 119), so far recorded only from the Behring Sea. The well-developed basal system (fig. 23 A, B, *b*) is several-layered and shows some anatomical differentiation (fig. 23 C). It bears a number of cylindrical unbranched erect fronds (fig. 23 B, *e*), reaching a height of 6 cm. and having much the same structure as in *Chordaria* (fig. 23 D); the unilocular sporangia (*u*) arise at the base of the few-celled cortical assimilators (*a*).

Acrothrix gracilis ((147) p. 65, (149) p. 93, (152) p. 53, (187) p. 33), which is referred to a distinct family by Kylin ((155) p. 43), is an infrequent sublittoral northern type (52, 187).[1] The uniaxial thallus is rather delicate, though well-branched, and attains a length of 30 cm. The main axial filament is terminated by a hair (fig. 24 A, *h*), with a sharply defined basal meristem (*g*), the segments of which (*af*) enlarge *without further division*. They produce whorls of primary laterals of limited growth, the basal cells (*b*) of which undergo marked increase in size and divide to form short large-celled perimedullary threads (*p*) constituting a continuous one-layered envelope around the axial filament. The second cell of each lateral usually develops an adaxial hair (*h*), whilst the others constitute a terminal assimilator (*a*). Other unbranched assimilators (*a*) arise from the basal cells of the laterals, as well as from the perimedullary cells, and in their entirety they form a narrow but complete envelope to the axial system. Later the perimedullary threads separate from the axial one, which either undergoes great attenuation (fig. 24 E, *af*) or disorganises so that the thallus becomes fistular (fig. 24 C). Branching is effected by the occasional development of a primary lateral into a new axial thread. Except for its intercalary growth and the presence of a terminal hair, *Acrothrix*

[1] Further species have been recorded from North America, Japan (295) and Norway ((160) p. 62).

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shows much resemblance to the Spermatochnaceae considered below. This is specially obvious in *A. novae-angliae* Taylor ((276), (279) p. 159).

The series of genera discussed in this section constitute a plexus of

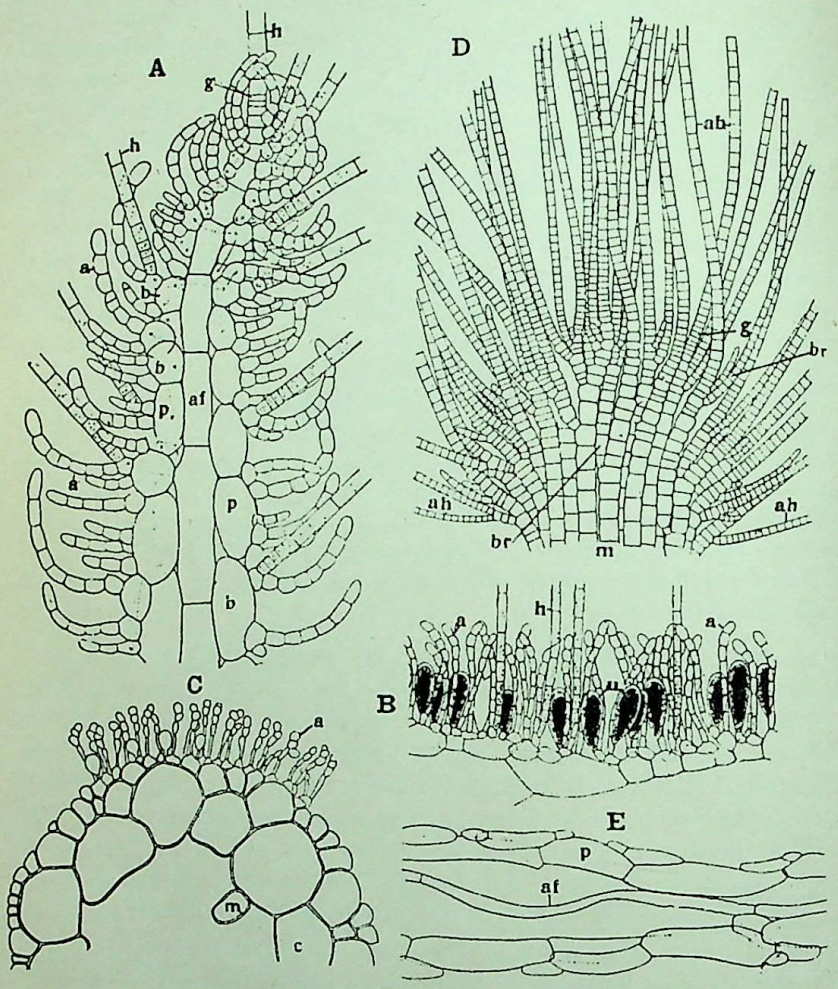

Fig. 24. A, B, E, *Acrothrix gracilis* Kylin; A, apex of thallus; B, peripheral part of longitudinal section of mature thallus, with unilocular sporangia; E, centre of mature thallus in longitudinal section. C, *A. novae-angliae* Taylor, part of cross-section of thallus. D, *Myriogloea Sciurus* (Harv.) Kuck., apex of thallus in longitudinal section. *a*, assimilator; *af*, axillary filament; *ah*, assimilatory hair; *b*, basal cell of lateral; *br*, branch; *c*, cortex; *g*, meristem; *h*, hair; *m*, axial threads; *p*, perimedullary threads; *u*, unilocular sporangium. (C after Taylor; the rest after Kuckuck.)

interrelated forms showing points of contact, on the one hand with Elachistaceae, on the other hand with Spermatochnaceae. They exhibit a progressive restriction of division to the subterminal meristem, as is shown by a comparison of *Mesogloea* with *Sphaero-*

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trichia and *Acrothrix*, all uniaxial types with monopodial branching. Among multiaxial forms *Myriogloea* and *Castagnea* show the same method of growth as *Mesogloea*, although *Castagnea* stands out by the sympodial build of its threads; *Chordaria*, on the other hand, seems to approach *Sphaerotrichia* in the restriction of division to the region of the meristem ((155) p. 60).

The often large unilocular sporangia (figs. 19 B, D; 21 D; 22 F; 24 B) are always borne laterally on or near the bases of the assimilators, while the plurilocular sporangia ((280) p. 237) are usually formed from the distal cells of the latter (fig. 21 A); in *Heterochordaria* ((256) p. 550), however, they are developed from the inner cells of the

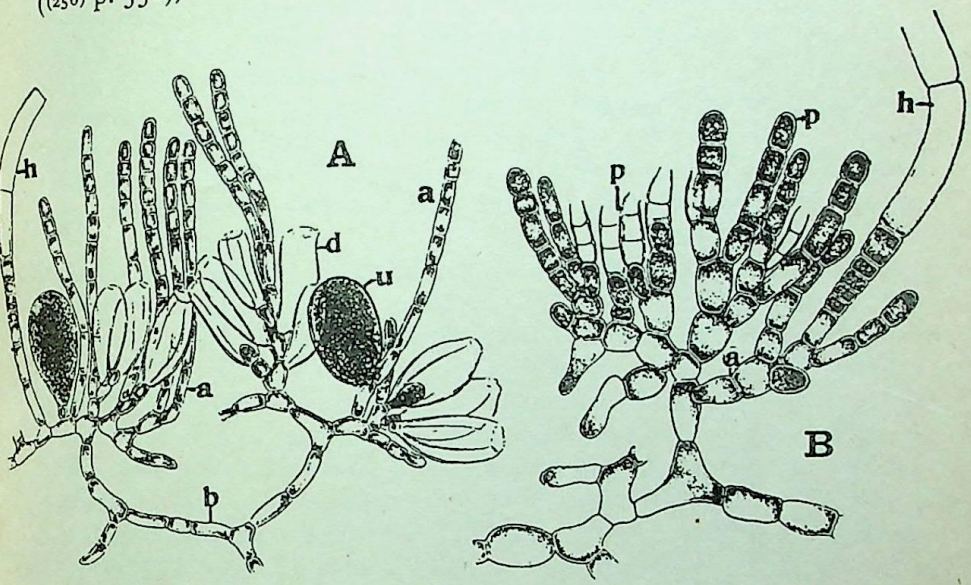

Fig. 25. *Strepsithalia Liagorae* Sauv. (after Sauvageau), A with unilocular, and B with plurilocular sporangia. *a*, assimilator; *b*, basal system; *d*, dehisced unilocular sporangium; *h*, hair; *p*, plurilocular and *u*, unilocular sporangium.

assimilators (fig. 22 G, *p*). Protection of the sporangia is most marked in *Chordaria*, where the often enlarged and thickened end-cells of the assimilators unite to form a protective cap (fig. 22 D), which is often supplemented by a layer of mucilage (cf. Laminariales).

Strepsithalia (214), an endophyte in various gelatinous Algae (*Mesogloea*, *Helminthocladia*), shows a loosely branched basal system bearing at intervals compact mucilaginous tufts composed of numerous branched assimilators (fig. 25 *a*). Hairs (*h*) are formed both on the creeping threads and on the lower cells of the assimilators. The latter closely resemble those of certain species of *Castagnea*, a resemblance which is heightened by the large unilocular sporangia borne at their base (fig. 25 A, *u*). The plurilocular sporangia (fig. 25 B, *p*) usually arise in the same position, but both kinds can also originate directly from the creeping threads. *Strepsithalia* is clearly a reduced form, which was

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referred by Kuckuck (147) to the Leathesiaceae, but a closer affinity with the Mesogloeaceae is perhaps to be suspected.

The Spermatochnaceae

The members of this family, while showing the same general structure as many Mesogloeaceae, are specially distinguished by apical growth of the axial filaments, the segments cut off from the hemispherical apical cell (fig. 26 C, *ac*) undergoing no further division. The uniaxial *Nemacystus*, in particular, shows much resemblance to *Acrothrix*, and it can hardly be doubted that here, as in other groups of Phaeophyceae (cf. p. 112), the trichothallic meristem has been replaced by a definite apical cell (cf. (175) p. 60). According to Kuckuck ((147) p. 65) the apical hair (fig. 24 A, *h*) is shed in older plants of *A. gracilis* and, subsequent to this, the cells of the axial thread exhibit enlargement only. If, however, the meristem remained active, we should have reached what is tantamount to apical growth and this apparently obtains in *A. novae-angliae* Taylor (276), a species which comes very close to *Nemacystus*.

This genus is probably the most primitive of the uniaxial Spermatochnaceae. In *N. flexuosus* (*N. ramulosus* Derb. et Sol. ((58) p. 269, (98) p. 366, (147) pp. 10, 68), a Mediterranean species with a branched filiform thallus, the basal cells of the whorled laterals (fig. 26 C, *l*) keep pace with the elongation of the segments of the axial thread, forming a large-celled envelope around it, much as in *Acrothrix*; later the thallus becomes hollow and the axial thread may disappear. The second cell of each lateral, as in other Spermatochnaceae (cf. fig. 27 B), produces an adaxial hair (fig. 26 C, *h*), while the remaining cells constitute a primary assimilator (*pa*, cf. *Acrothrix*). The large-celled perimedullary envelope is augmented by the outgrowth of short threads (*d*) which bear numerous secondary assimilators (*sa*). The two kinds of sporangia arise laterally from the lower cells of the assimilators (fig. 26 F). In the Japanese *N. decipiens* (*Mesogloea decipiens* Suring. (266) p. 75; *Cladosiphon decipiens* Okam. (177) pl. 89) the thallus remains solid.

Spermatochnus paradoxus (*Stilophora Lyngbaei* Harv. (95) pl. 237), a deep-water annual growing on sand or mud, has a firm dichotomously branched thallus which is fistular in the older parts (fig. 27 A). The axial thread ((198) p. 66, (200) p. 53), arising from the usual prostrate base, bears alternating whorls of generally four clavate assimilators (fig. 27 F, *a*) at the upper end of each segment (fig. 27 B, *a*). The basal cell (*b*) of each such assimilator at an early stage grows out on its under side into a branched cortical thread (fig. 27 B, F, *d*), which keeps pace with the increasing elongation of the axial segment so that the group of threads from each whorl completely envelops the part of the segment below. This is followed by the

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outgrowth from the epibasal cells of similar threads (fig. 27 B, *d'*) which cover those first formed. Subsequent periclinal division of the cells of the outer threads results in a firm, several-layered envelope

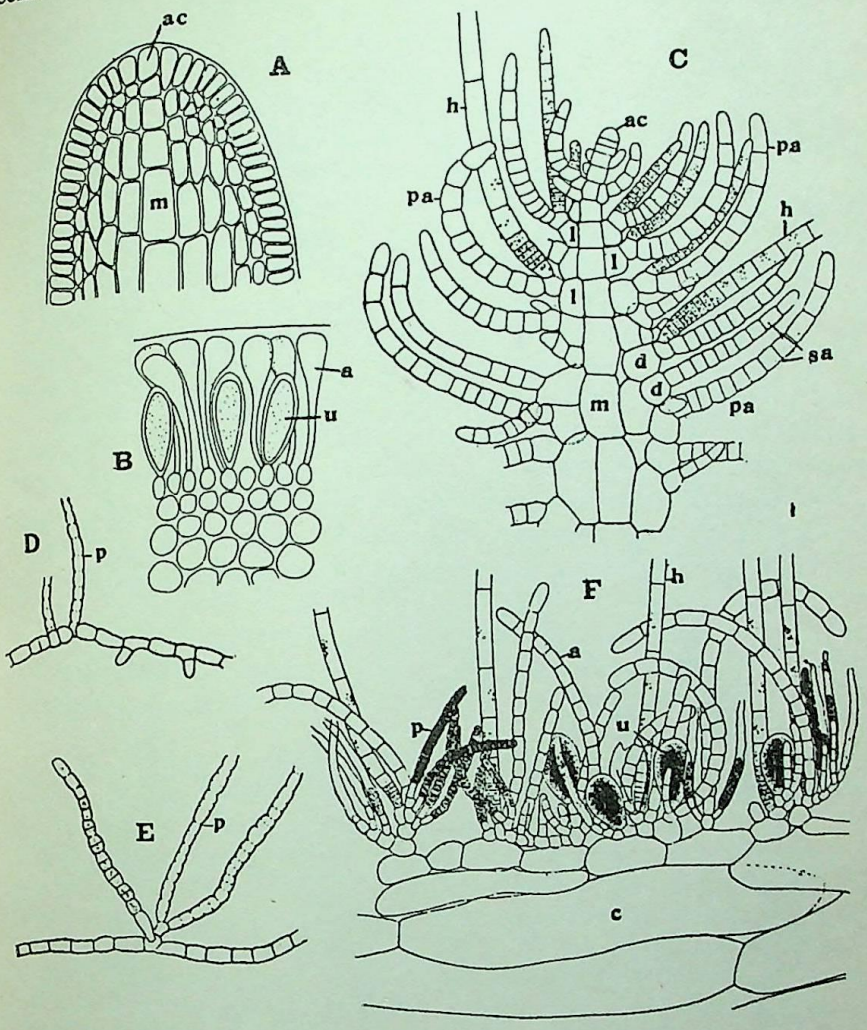

Fig. 26. A, B, *Chordariopsis capensis* (Ag.) Kyl.; A, apex in longitudinal section; B, small part of periphery of transverse section, with unilocular sporangia. C–F, *Nemacystus flexuosus* (Ag.) Kyl.; C, apex of thallus; D, E, plethysmothalli; F, periphery of longitudinal section of mature thallus, with sporangia. *a*, assimilator; *ac*, apical cell; *c*, cortex; *d*, descending filaments of lateral; *h*, hair; *l*, lateral; *m*, axial thread; *p*, plurilocular and *u*, unilocular sporangium; *pa*, primary and *sa*, secondary assimilator. (A, B after Kylin; C, F after Kuckuck; D, E after Sauvageau.)

(fig. 27 C, E, L, *co*) around the axial thread. Later, owing to the extensive peripheral growth, the axial thread (fig. 27 D, E, L, *m*), separates from the surrounding envelope, the resulting hollow (*c*)

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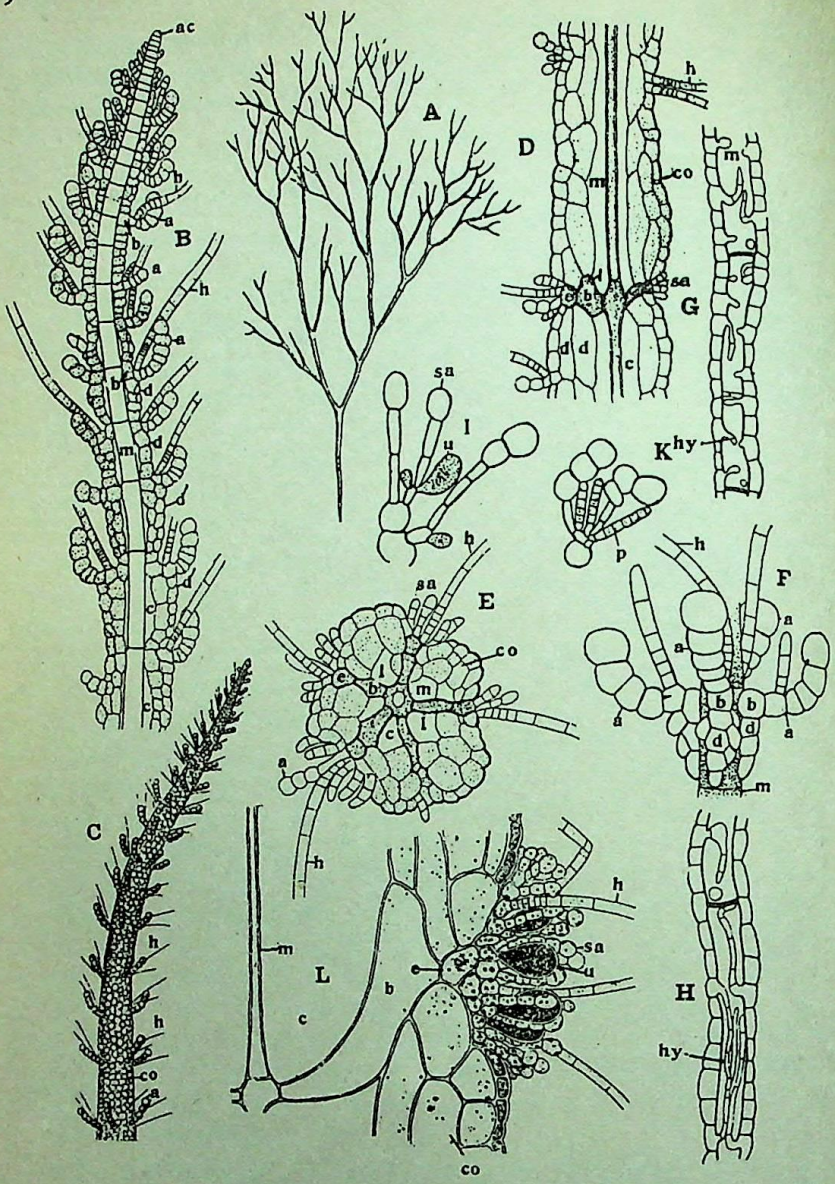

Fig. 27. *Spermatochnus paradoxus* Kütz. A, habit; B, apical part of thallus in longitudinal section; C, the same, external view; D, longitudinal section of older part of thallus; E, transverse section of relatively young part of the thallus; F, apex of thallus; G, H, axial thread with hyphae; I, K, assimilators with unilocular and plurilocular sporangia respectively; L, small part of longitudinal section through an older thallus, with a sorus of unilocular sporangia. *a*, assimilator; *ac*, apical cell; *b*, basal cell of lateral; *c*, cavity; *co*, cortex; *d*, descending filament from basal cell, *d'* from epibasal cell; *e*, epibasal cell of lateral; *h*, hair; *hy*, hypha; *l*, lateral; *m*, axial thread; *p*, plurilocular and *u*, unilocular sporangium; *sa*, secondary assimilator. (A after Newton; G, H after Jönsson; I, K after Sauvageau; the rest after Reinke.)

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being occupied by aqueous mucilage. The persisting axial thread (fig. 27 L, *m*) remains connected to the cortical envelope by the elongate basal cells (*b*) of the primary assimilators.[1] Branching is effected by one of the primary laterals developing into a new axial thread. According to Jönsson ((110) p. 15) the cells enveloping the axial thread may give rise to hyphae which penetrate the walls and later the cell-cavities of the former (fig. 27 G, H, *hy*); their cells may contain chromatophores (cf. *Desmarestia*, p. 186).

When the reproductive phase sets in (fig. 27 D, E, L), the projecting portions of the assimilators are shed and only the basal (*b*) and epibasal (*e*) cells remain. From the latter hairs (*h*) and secondary assimilators (*sa*) are produced, the uni- and plurilocular ((246) p. 122) sporangia usually arising as lateral outgrowths from the lower cells of these assimilators (fig. 27 I, K). The sori thus formed occupy the positions of the former primary assimilators, but similar sori can subsequently originate at any point on the cortex.

Spermatochnus departs appreciably from the forms hitherto considered in the fact that the assimilators are of quite subordinate importance until the time of reproduction, the photosynthetic region of the vegetative plant being constituted by a cortex formed by the close juxtaposition of cortical threads produced from the lower cells of the whorled laterals. In this respect it resembles the Desmarestiales. The abundant production, in the reproductive phase, of assimilators, which, as in Mesogloeaceae, act both as a protection for the developing sporangia and as a local photosynthetic apparatus, is again a feature seen in many advanced members of the Brown Algae.

Stilophora and *Halorhiza* are multiaxial, although it is uncertain whether this structure is primary or secondary (cf. fig. 28 F).[2] The peripheral cells of the axis bear curved assimilators (fig. 28 A, C, F, *a*) which overtop the summit, although more or less widely separated in the older parts as a result of the marked elongation of the axial cells. The cortical envelope (fig. 28 C, *co*) is formed in the same way ((198) p. 70, (200) p. 55) as in *Spermatochnus* (cf. fig. 28 F), its peripheral cells finally dividing to form a small-celled superficial layer (fig. 28 E, *s*) bearing the simple or branched secondary assimilators (*sa*); these are either uniformly distributed (*Halorhiza*) or appear in localised areas (*Stilophora*). They bear the two kinds of sporangia ((280) p. 238) on their lower cells (fig. 28 D, E, *p*). In the older parts the medullary threads

[1] *Spermatochnus Lejolisii* Reinke (*Stilophora Lejolisii* Thur.) is referred by Kuckuck ((147) pp. 11, 70) to a distinct genus *Stilopsis*, distinguished by the sympodial growth of the axial thread which becomes surrounded by a large-celled envelope as in *Nemacystus*. The numerous assimilators are short and papillate (cf. also (155) p. 50).

[2] Kuckuck ((147) pp. 11, 68) gives rather contradictory accounts of these forms and the description given above is based on that of Kjellman ((121) p. 230).

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separate, the central hollow being occupied by hyphae which are outgrowths from the medullary cells (cf. also (36) p. 87).

Stilophora rhizodes ((95) pl. 70) is a not uncommon annual on diverse substrata near low-water mark and favours situations where there is an

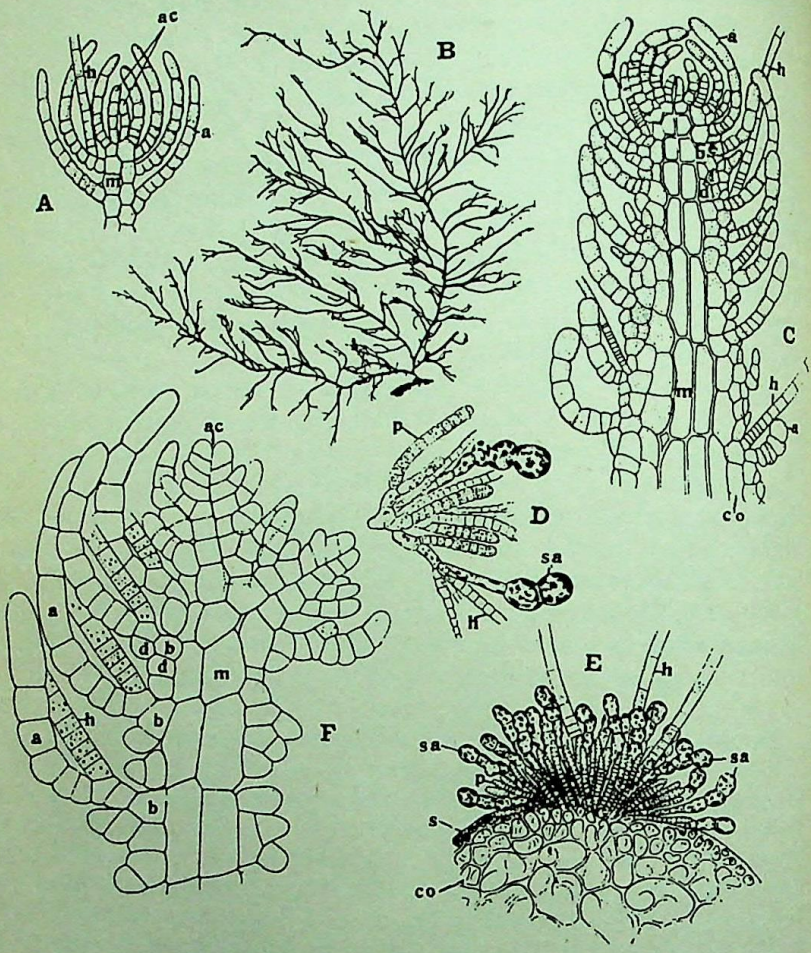

Fig. 28. *Stilophora rhizodes* J. G. Ag. A, apex of thallus; B, habit; C, F, longitudinal sections of apex of thallus; D, fertile tuft with plurilocular sporangia; E, peripheral part of thallus with a similar fertile tuft. *a*, assimilator; *ac*, apical cell; *b*, basal cell of lateral; *co*, cortex; *d*, descending filament; *e*, epibasal cell of lateral; *h*, hair; *m*, axial threads; *p*, plurilocular sporangia; *s*, surface layer of thallus; *sa*, secondary assimilators. (A, C after Reinke; B photo. R. Cullen; D, E after Thuret & Bornet; F after Kuckuck.)

influx of fresh water into the sea. The thallus (fig. 28 B), up to 65 cm. long, shows subdichotomous branching, the rounded wart-like sori being scattered over the whole surface. *Halorhiza vaga* Kütz. is so far known only from the Baltic.

Kylin ((155) p. 54) establishes the genus *Chordariopsis* for the South

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African *Chordaria capensis* Aresch. (cf. (147) p. 62), a uniaxial form distinguished by its firm parenchymatous structure (fig. 26 A). Assimilators are completely lacking on the vegetative parts, while on the fertile tracts (fig. 26 B) they appear as clavate, usually one-celled, structures (*a*) forming a protection for the unilocular sporangia (*u*) which arise from the peripheral cells.

The Genus Splachnidium

There is every reason to believe ((147) p. 9, (260) p. 287) that this anomalous monotypic genus is a specialised member of the haplostichous Ectocarpales. *S. rugosum* ((93) pl. 14; fig. 29 A), with a gelatinous, monopodially branched, hollow thallus attached by a basal disc, is a perennial alga of the Southern Hemisphere (Cape of Good Hope, Australasia). In the past it has usually been referred to Fucales owing to the occurrence of the unilocular sporangia (fig. 29 C) in conceptacles, although the considerable differences were already clearly pointed out by Mitchell and Whitting (170). The "apical cell" recognised by earlier investigators ((93) pl. 14, (156), (170), (201)) is an endophytic *Codiolum* ((147) p. 78, (260) p. 282) which appears to be invariably present (fig. 29 B, D, *c*).

The apices of the thallus-branches (fig. 29 D) are occupied by monopodially branched threads (*t*), capped by numerous short, clavate assimilators (*a*). The axial threads grow by a subapical meristem (*me*), but separate widely a short distance behind the apex; as in *Leathesia*, however, they remain connected by anastomoses bridging the large mucilaginous interspaces (fig. 29 B, *m*), which are also traversed by numerous branching hyphae (*hy*). In the older parts the assimilators are shed and the surface is formed by a compact cortex (*co*) of small cells.

The conceptacles appear to originate in the immediate neighbourhood of the apex by localised cell-division leading to overarching of certain parts of the surface. The centres around which the conceptacles arise are usually occupied by a *Codiolum*-individual (fig. 29 D). This may imply that the presence of the endophyte exerts a stimulus[1] or the association may be due to a local alteration of the surface facilitating colonisation. Hairs are restricted to the inner surface of the conceptacles, although they project from the aperture, much as in Fucales (fig. 29 C). The large unilocular sporangia (*u*) arise successively from the cells forming the inner lining (*w*). Laing has observed the escape of zoospores (see (174)).

Splachnidium constitutes a striking example of parallel development, the conceptacles though so similar to those of Fucales being borne on a thallus with an altogether different structure and mode of growth.

[1] Nienburg in *Zeitschr. Bot.* **13**, 181, 1921.

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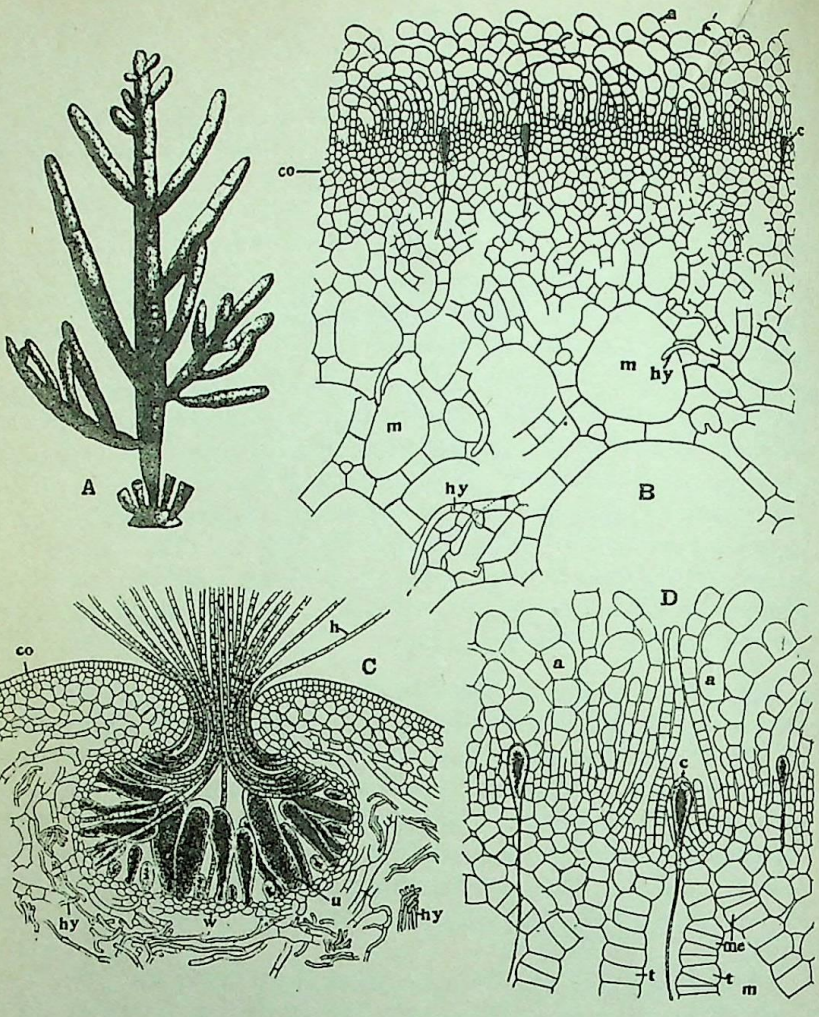

Fig. 29. *Splachnidium rugosum* (L.) Grev. A, habit; B, apical part of a branch in longitudinal section; C, section of a conceptacle, with unilocular sporangia; D, longitudinal section through apex of thallus. *a*, assimilator; *c*, *Codiolum*-plants; *co*, cortex; *h*, hair; *hy*, hyphae; *m*, mucilaginous interspaces; *me*, subapical meristem of axial thread; *t*, axial threads; *u*, unilocular sporangium; *w*, wall of conceptacle. (A after Mitchell; the rest after Kuckuck.)

(*c*) The Polystichous Ectocarpales

The formation of a thallus by longitudinal septation of a primary filament is infrequent, although found in Ulvaceae and Prasiolaceae among Chlorophyceae and in Bangiales among Rhodophyceae. In the Phaeophyceae, on the other hand, it has resulted in the evolution of the highly specialised Laminariales and Fucales. On these grounds it might appear justifiable to treat the polystichous Ectocarpales as a

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separate order. Their simplest representatives are, however, but little removed from Ectocarpaceae, both in structure and reproduction, so that a separation of the polystichous forms from other Ectocarpales would be artificial. The early stages of development, moreover, are ectocarpoid and evidently heterotrichous (figs. 31 A; 33 K), one or usually several of the erect threads giving rise to mature thalli.

Occasional longitudinal division is found in diverse Ectocarpaceae (p. 55), and this tendency, though little apparent in the vegetative parts of the haplostichous forms, is shown by the frequent multiseriate character of the plurilocular sporangia. The diverse genera to be considered form a closely related assemblage and their segregation into families presents considerable difficulties. The grouping adopted below, based on morphological characters, is largely one of convenience.

Punctariaceae

One of the simplest polystichous forms is *Phloeospora* ((147) p. 82, (167)). The erect filaments of *P. brachiata* Born. (*Ectocarpus brachiatus* Harv. (95) pl. 4), a widely distributed but rather rare summer epiphyte on *Rhodymenia palmata*, arise from a system of endophytic threads (fig. 30 G, *e*) and are at first uniseriate (fig. 30 B). Longitudinal walls appear at rather regular intervals (*l*) and, at these points, branches (*br*) and, at a later stage, reproductive organs arise; the branches are commonly opposite. Longitudinal septation later extends also to other parts (fig. 30 A), but the apices (*a*) of the filaments remain permanently uniseriate. Division of the primary cells is sometimes plentiful (fig. 30 C) and leads to a multiseriate, though slender, thallus, occasionally with a slight differentiation in size between central and peripheral cells. Rhizoids, which often develop in considerable numbers from the lower cells, serve to strengthen the attachment to the substratum (fig. 30 G).

Unilocular sporangia develop as embedded structures directly from the peripheral cells at and near the points of branching (fig. 30 A, D, E, *u*), while plurilocular sporangia are rare ((167) p. 9). Sporangia commonly develop in individuals which are still for the most part uniseriate, a feature encountered in most of the genera considered in the following pages.

Phloeospora[1] agrees with the more typical Punctariaceae in the lack of any marked differentiation among the cells and the immersed position of the sporangia. Several genera exhibit a surface-development and betray a considerable degree of parallel with the Ulvaceae.

[1] The related genus *Xanthosiphonia* ((7) p. 112, (122) p. 159, (257) p. 28) is distinguished by alternate branching and restriction of the plurilocular sporangia to special branches in which they form a complete envelope to the central sterile cells. Unilocular ones are unknown.

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The leafy thalli of *Punctaria* ((149) p. 70, (239) p. 334, (281) p. 13),[1] which usually grow in tufts, are almost exact replicas of *Ulvas*. In *P. latifolia* ((95) pl. 8), a frequent annual lithophyte, the olive-brown fronds, which may reach a length of 40 cm., taper into a short slender stalk terminating in a basal attaching disc (fig. 32 C). The mature

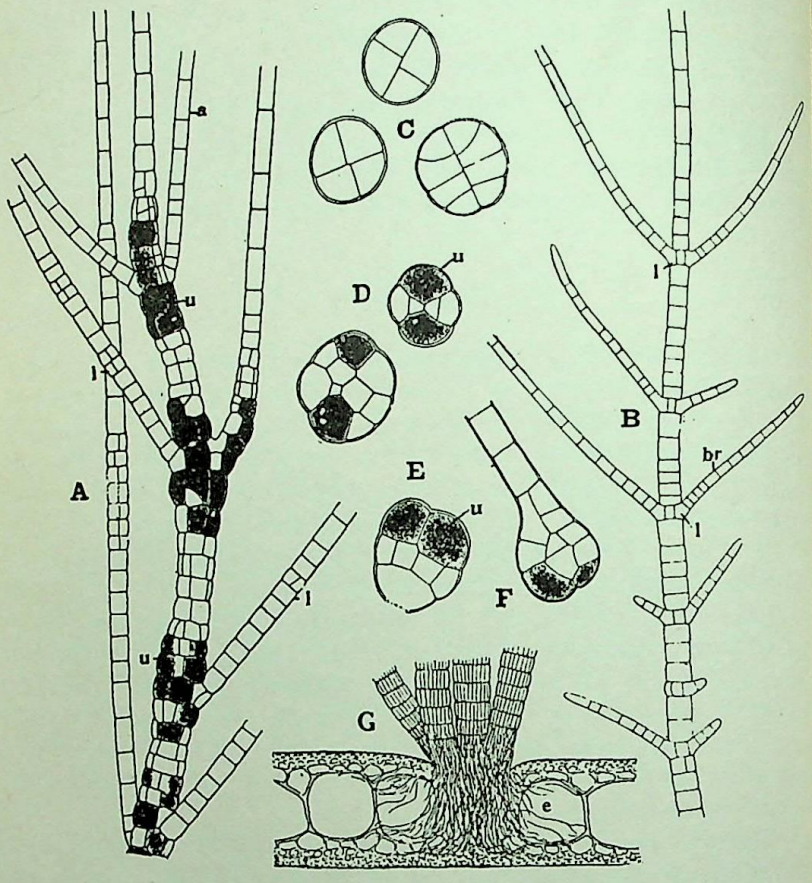

Fig. 30. *Phloeospora brachiata* Born. (after Kuckuck). A, part of a plant with unilocular sporangia; B, young vegetative thread; C–F, transverse sections of thallus at different levels, in F passing through a branch; G, base of an older plant, with endophytic rhizoids (*e*). *a*, apical parts of branches; *br*, branch; *l*, regions of commencing longitudinal division; *u*, unilocular sporangium.

thallus consists of up to seven layers of cells (fig. 31 L), of which the inner are often longer than the outer ((203) p. 72). At certain points the superficial cells grow out into colourless sheathed hairs (*h*), forming tufts which often appear slightly immersed. The embedded

[1] Agardh (8) groups the species of *Punctaria* into several genera (cf. (121) p. 155), which have not met with general recognition.

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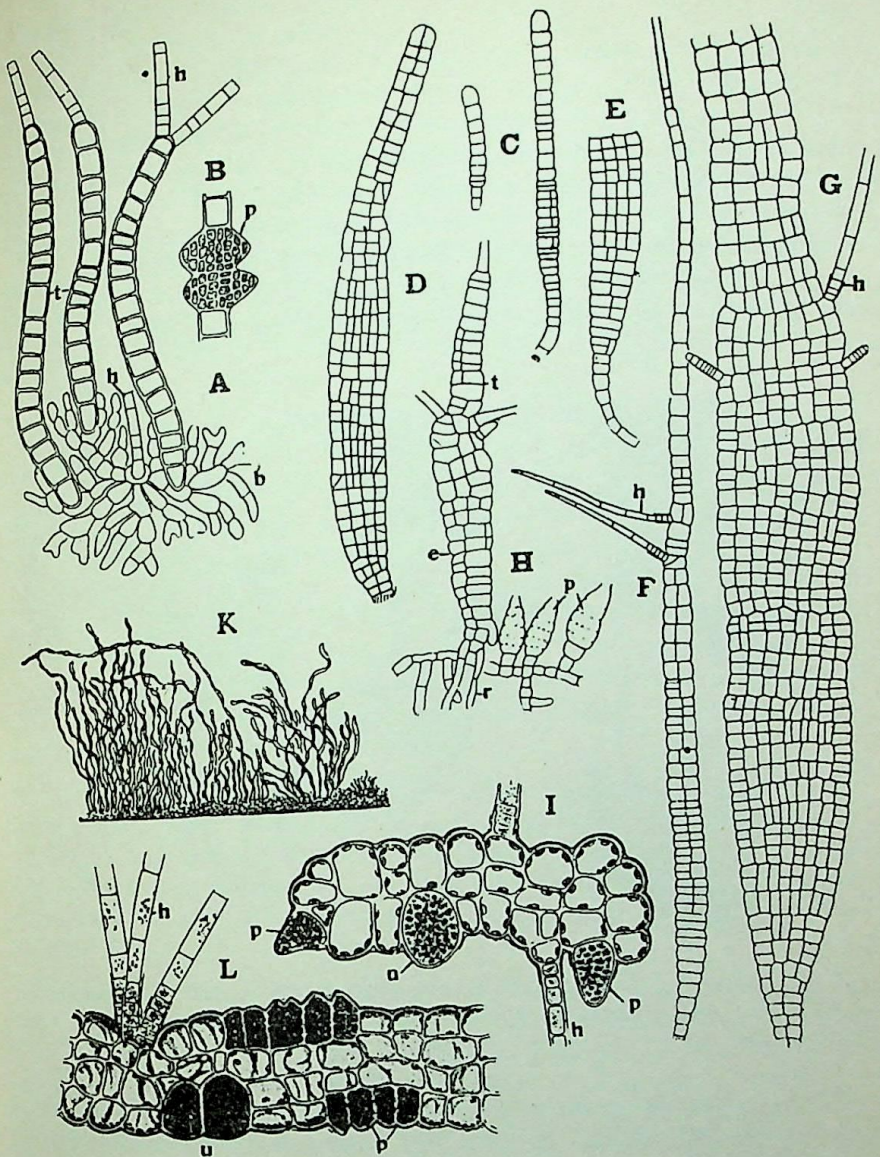

Fig. 31. A, B, I, K, *Desmotrichum undulatum* (J. Ag.) Reinke; A, young plant derived from the swarmer of a plurilocular sporangium; B, plurilocular sporangia in erect thread of same; I, transverse section of mature thallus, with the two kinds of sporangia; K, habit. C–H, L, *Punctaria latifolia* Grev.; C–G, progressive stages in the development of the mature thallus; H, plethysmothallus with dehisced plurilocular sporangia and a young thallus; L, transverse section of mature thallus, with the two kinds of sporangia. *b*, basal and *e*, erect system; *h*, hair; *p*, plurilocular and *u*, unilocular sporangium; *r*, rhizoid; *t*, developing thallus. (A, B after Kylin; I, K after Reinke; L after Thuret & Bornet; the rest after Sauvageau.)

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sporangia form sori, the unilocular ones (*u*) differentiating when the thallus is only two-layered and becoming immersed by further division of the surrounding cells, while the plurilocular ones (*p*) develop later and project slightly above the surface. The sori of plurilocular sporangia, in particular, appear as dots to the naked eye.

The young stages ((239) p. 338) are simple unbranched uniseriate filaments arising from a creeping base (fig. 31 C). Longitudinal division leading to surface expansion soon commences (fig. 31 D–F), although apex and base remain uniseriate. The basal part soon becomes overgrown by rhizoids (cf. fig. 31 H, *r*) produced from the lower cells. Marginal hairs (fig. 31 G, *h*) appear before the superficial ones.

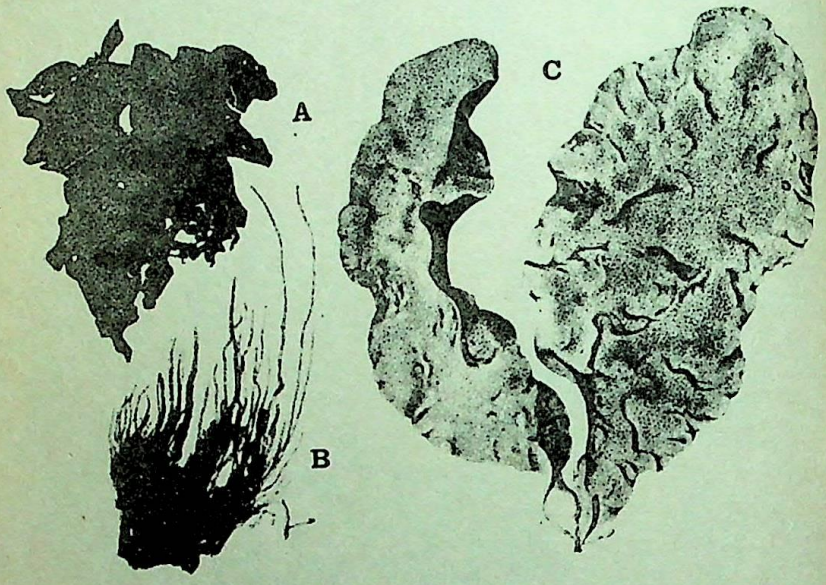

Fig. 32. Habits of A, *Omphalophyllum ulvaceum* Rosenv.; B, *Phaeosaccion Collinsii* Farl.; C, *Punctaria latifolia* Grev. (A, B after Rosenvinge; C after Thuret & Bornet.)

Forms having the same essential structure (fig. 31 I) but possessing a ribbon-shaped thallus (fig. 31 K) are often placed in a separate genus *Desmotrichum* ((20) p. 17, (158) p. 43, (198) p. 55, (258) p. 5; incl. *Rhabdinocladia* (248)). The young stages of *D. undulatum* (fig. 31 A), a rare epiphyte found near low-tide level, show evident heterotrichy ((152) p. 36, (196) p. 111), the prostrate base (*b*) producing a few hairs (*h*) and a number of erect uniseriate threads (*t*) bearing one or more apical hairs. In cultures these threads may form plurilocular sporangia (fig. 31 B), and such stages recall the alga described as *D. balticum* Kütz. ((86) p. 37, (199) p. 15) in which the filaments, though showing considerable longitudinal septation in later stages, do not exceed a centimetre in height and bear plurilocular sporangia either in an intercalary position or as lateral outgrowths. This is possibly but a precociously fertile juvenile

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stage of *D. undulatum* (cf. (152) p. 38). Lund ((164) p. 34) records structures like the ascocysts of *Ascocyclus* on certain individuals of *D. balticum*.

The subantarctic *Corycus* ((117) p. 3, (257) p. 31, (261) p. 35) has a club-shaped thallus which is solid below and hollow above. In other respects it resembles *Punctaria*.

The parallel between Punctariaceae and Ulvaceae is also illustrated by *Phaeosaccion* ((25), (62), (202) p. 874), which has a tubular thallus simulating that of *Enteromorpha* (fig. 32 B). The wall of the tube is composed of a single layer of cells, each with a lobed chromatophore. The plurilocular sporangia are commonly formed only by a single division of the vegetative cell. In *Omphalophyllum* ((202) p. 872; fig. 32 A) the thallus is probably at first a hollow sack, which later tears open irregularly (cf. *Monostroma*).

The early stages of *Litosiphon* ((159), (160) p. 66) *pusillus* ((95) pl. 270) resemble an unbranched *Phloeospora* (fig. 33 F, J), but there is a greater degree of ultimate differentiation, since the central cells are much larger (cf. fig. 33 D, *a*) than the peripheral ones which contain the bulk of the chromatophores. Hairs occur scattered over the surface of the thallus (fig. 33 A). The immersed sporangia cover considerable areas (fig. 33 A), the plurilocular ones developing before the unilocular ((152) p. 26, (239) p. 352). The basal parts continue to elongate after the upper have become fertile. The unbranched filaments of *L. pusillus* are frequent on *Chorda filum*, often covering the latter in late summer.

In *L. filiformis* (Reinke) Batt. (*Pogotrichum filiforme* Reinke (108), (109), (139) p. 360, (200) p. 62, (202) p. 869), an epiphyte on *Laminaria* (fig. 33 E), the central cells are exceptionally large (fig. 33 D). Kuckuck (139), (146) found plurilocular sporangia arising directly from the prostrate system, individuals exhibiting this phenomenon commonly failing to produce erect threads.

Stictyosiphon (incl. *Cladothele* Hook. & Harv. (173)) differs principally in the extensive ramification of its thallus; the numerous branches end in colourless hairs. *S. tortilis* Reinke ((200) p. 48, (204)) is found on diverse substrata in the littoral and sublittoral regions. Rosenvinge ((204) p. 4) describes the basal disc (fig. 33 H) as parenchymatous and composed of large quadrangular cells arranged in vertical rows. The structure of the erect thallus (fig. 33 B, C) and the arrangement of the reproductive organs does not differ in any appreciable respect ((139) p. 363) from that of *Litosiphon filiformis*. In *S. soriferus* (Reinke) Rosenv. ((204) p. 9; *Kjellmania sorifera* Reinke[1] (198) p. 59, (199) pl. 3) the sporangia are either embedded (fig. 33 I) or form projecting sori. There can be little doubt that the genera *Litosiphon* and *Stictyosiphon*

[1] Other synonyms included by Rosenvinge are: *S. Corbieri* Sauv. ((239) p. 298); *S. adriaticus* Kuck. non Kütz. ((147) p. 81; cf. also (64) p. 156). Levring ((160) p. 71, (162) p. 53), however, holds that Reinke's form is a distinct species and that Rosenvinge's *S. soriferus* is a form of *S. subarticulatus* (Aresch.) Reinke.

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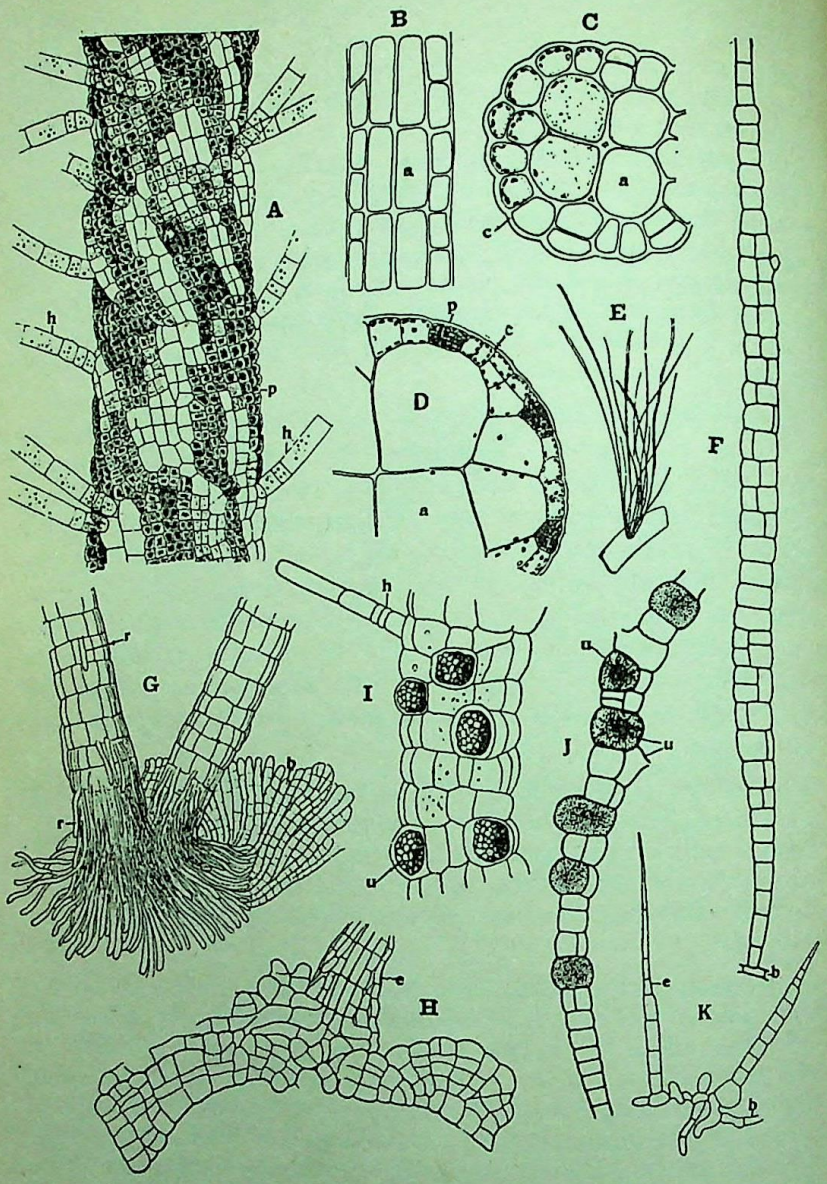

Fig. 33. A, F, J, K, *Litosiphon pusillus* Harv.; A, part of an old plant with plurilocular sporangia; F, young stage; J, same with unilocular sporangia; K, germling from swarmer of plurilocular sporangium. B, C, H, *Stictyosiphon tortilis* Reinke; B, longitudinal and C, transverse sections of vegetative thallus; H, vertical section of basal stratum. D, E, *Litosiphon* (*Pogotrichum*) *filiformis* (Reinke) Batt.; D, transverse section with plurilocular sporangia; E, habit of fertile plant. G, I, *Stictyosiphon soriferus* (Reinke) Rosenv.; G, base of plant; I, thread with unilocular sporangia. *a*, axial cell; *b*, basal system; *c*, cortex; *e*, erect thallus; *h*, hair; *p*, plurilocular and *u*, unilocular sporangium; *r*, rhizoid. (A, E after Kuckuck; F, J, K after Sauvageau; the rest after Rosenvinge.)

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are closely allied, although Kjellman ((121) pp. 201, 208) placed them in distinct families on the grounds that in the former intercalary division persists longest at the base, whilst in the latter it persists longest below the apex.

Asperococcaceae

Petalonia[1] (*Phyllitis*) and *Scytosiphon*, while showing essentially the same thallus-structure, differ from the genera above discussed in the manner in which the reproductive organs are borne. *Petalonia Fascia* (*Phyllitis Fascia* (Müll.) Kütz.; *P. caespitosa* Le Jol. (281) p. 9; *Laminaria Fascia* (95) pl. 45) has undulate, greenish or olive-brown thalli which may reach a length of 30 cm. and are narrowed basally into a short flattened stalk (fig. 34 A); it is usually found near low-water mark. Sections ((58) p. 265, (195), (251) p. 110) show a central medulla (fig. 34 E, *m*) of large and somewhat elongate, colourless cells, interspersed with hyphae (*hy*), and a cortex (*c*) of small cells. The early stages (fig. 34 F) are of the usual heterotrichous type; those described by Yendo (297) are probably pathological.

Scytosiphon Lomentaria (*Chorda Lomentaria* Lyngb. (95) pl. 285), common in rock-pools between tide-levels, has narrow unbranched fistular thalli, up to 50 cm. long, with occasional constrictions and gradually tapering at base and apex; they generally grow in tufts (fig. 34 G), in which smaller individuals showing little or no constriction are intermingled with the larger ones. The mature thalli ((1) p. 334, (199) p. 17) originate from the primary heterotrichous stages (fig. 34 B, C) by longitudinal division of the erect threads (cf. also (286)), each of which terminates in a hair. Later similar hairs arise in a lateral position (fig. 34 B); in the mature thallus they may occupy pits ((257) p. 34) like those of *Colpomenia* (p. 111). As the fronds enlarge, the central cells undergo marked increase in size (fig. 34 D) and produce a long-celled medulla (*m*), while the peripheral ones divide abundantly to form the 1–2-layered photosynthetic cortex (*c*). The subsequent separation of the medullary cells fails to occur at fairly regular intervals, where the central hollow is interrupted.

Both *Petalonia* and *Scytosiphon* produce only plurilocular sporangia, which are formed by outgrowth of the superficial cells over considerable areas. In *Petalonia* (fig. 34 E) the densely packed sporangia (*p*) possess 4–6 rows of compartments, while the sori of *Scytosiphon* (fig. 34 D) are interrupted by occasional large, ovoid or pyriform cells (paraphyses, *a*) which overtop the sporangia (*p*).

Striaria attenuata ((95) pl. 25) is a sublittoral epiphyte with cylindrical thalli (fig. 35 A) reaching a length of 50 cm. The commonly opposite branches (sometimes in whorls of three) taper to either extremity and, in the fruiting condition, usually show a transverse

[1] Setchell and Gardner ((256) p. 535) use the name *Ilea*.

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banding due to the sori of unilocular sporangia (fig. 35 D, *u*); each branch terminates in a hair. Longitudinal septation of the primary filament (fig. 35 B) sets in at an early stage ((153) p. 16), but intercalary growth continues for a long time in the subapical region (*m*). The large central cavity (fig. 35 C) in the mature thallus is usually sur-

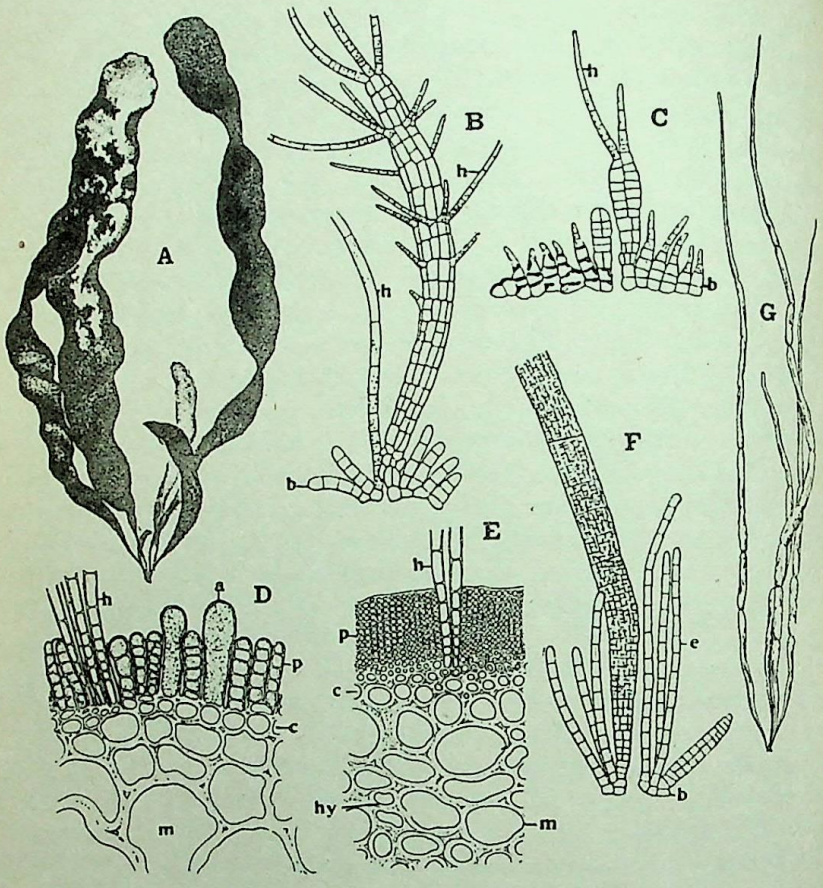

Fig. 34. A, E, F, *Petalonia Fascia* (Müll.) Kuntze; A, habit; E, periphery of transverse section of thallus, with plurilocular sporangia; F, young plants. B–D, G, *Scytosiphon Lomentaria* (Lynbg.) Ag.; B, older and C, younger germlings; D, periphery of transverse section of thallus with a sorus; G, habit. *a*, paraphysis; *b*, basal and *e*, erect systems; *c*, cortex; *h*, hair; *hy*, hyphae; *m*, medulla; *p*, plurilocular sporangia. (A after Thuret & Bornet; B, C, F after Kuckuck; the rest after Taylor.)

rounded by only two layers of cells ((200) p. 50). The sessile unilocular sporangia (fig. 35 C, D, *u*) are intermingled with unicellular paraphyses (*a*) and hairs (*h*).

In the projecting sori of certain allied genera multicellular assimilators are associated with the sporangia. One of the simplest of these

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is *Myriotrichia* ((22) p. 311, (41), (64) p. 292, (86) p. 41, (141), (219) p. 269), some forms of which barely depart from the filamentous condition (fig. 36 D). Its species are minute epiphytes (fig. 36 I, *m*), which never exceed a few centimetres in length and form dark, olive-brown, rather soft tufts. *M. clavaeformis* ((95) pl. 101), not uncommon on *Scytosiphon*

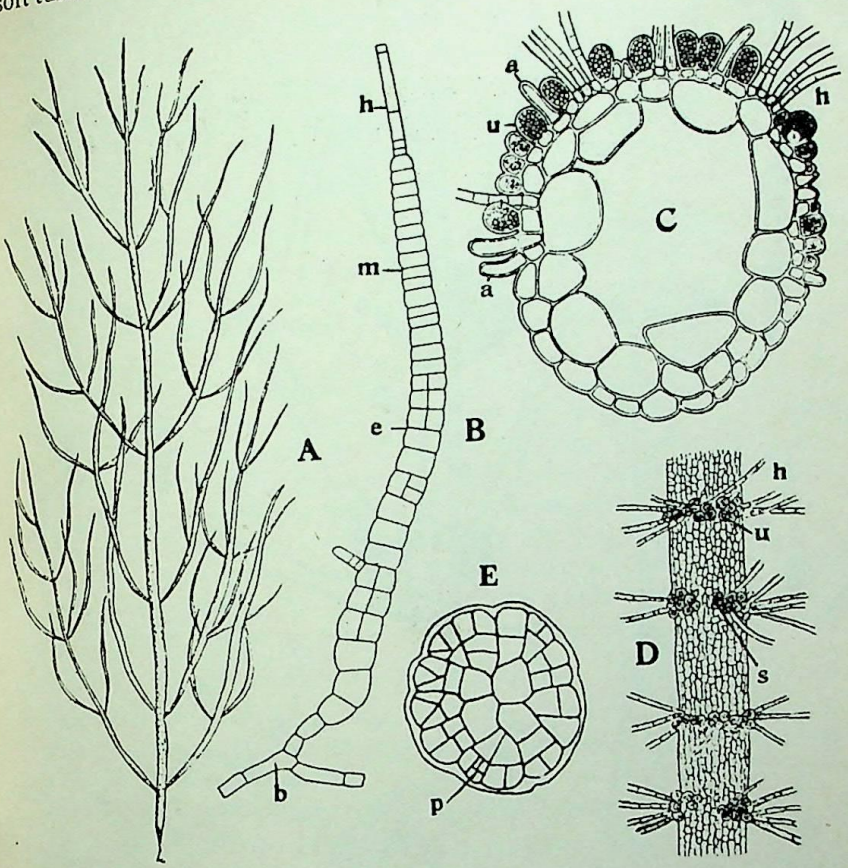

Fig. 35. A–D, *Striaria attenuata* (C. Ag.) Grev.; A, habit; B, germling; C, transverse section of mature thallus, with sporangia; D, external view of thallus, with sori. E, *Isthmoploea sphaerophora* (Carm.) Kjellm., transverse section of thallus, with young plurilocular sporangia. *a*, paraphysis; *b*, basal system; *e*, erect thallus; *h*, hair; *m*, meristem; *p*, plurilocular and *u*, unilocular sporangium; *s*, sorus. (A after Newton; B after Kylin; C, D after Reinke; E after Jönsson.)

Lomentaria and other Algae, has a somewhat club-shaped axis (fig. 36 A, *a*), which is capped by a hair and is uniseriate below, where intercalary division continues for some time. Short, sometimes whorled, assimilators (*a*), intermingled with occasional colourless hairs (*h*), occur in large numbers; in rare instances one of the assimilators develops into a branch. The uni- and plurilocular sporangia, generally found on distinct individuals, arise directly (fig. 36 B, C) from the

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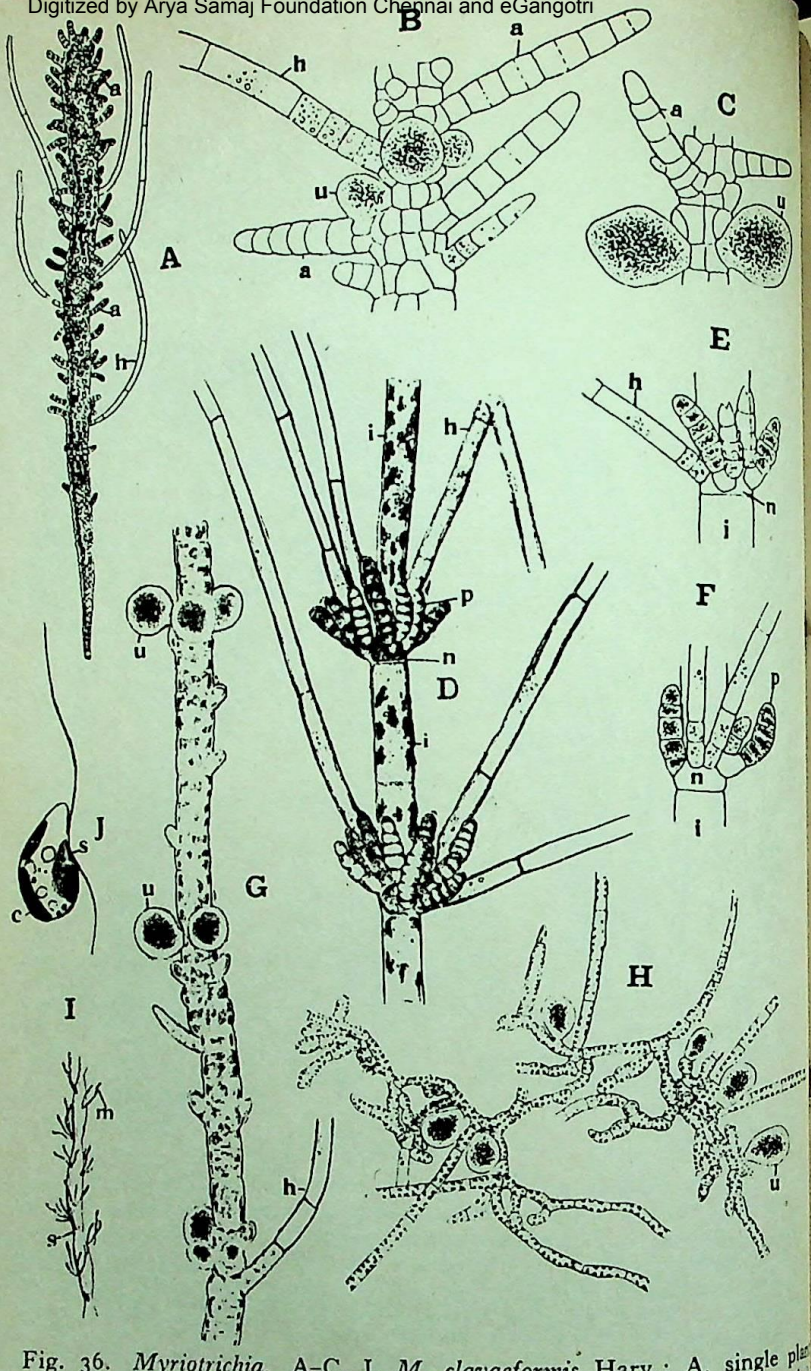

Fig. 36. *Myriotrichia.* A–C, I, *M. clavaeformis* Harv.; A, single pla... enlarged; B, C, parts of plants with unilocular sporangia; I, plants (*m*... natural size, on *Scytosiphon* (*s*). D–H, *M. repens* (Hauck) Karsak.; D, pa... of a thread with two zones of hairs with plurilocular sporangia; E, F, deta... of two such zones; G, part of a thread with unilocular sporangia; H, bas... stratum, with sporangia. J, *M. filiformis* (Griff.) Harv., swarmer from plur... locular sporangium. *a*, assimilator; *c*, chromatophore; *h*, hair; *i*, internod... *n*, node; *p*, plurilocular and *u*, unilocular sporangium; *s*, stigma. (A, J afte... Newton; the rest after Kuckuck.)

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superficial cells, being either scattered or arranged in ill-defined annular zones. According to Kuckuck ((141) p. 73) assimilators may be altogether lacking in plants bearing plurilocular sporangia. Both in *M. clavaeformis* and *M. repens* unilocular sporangia are sometimes borne directly on the prostrate system (fig. 36 H; (112) p. 443, (141) pp. 61, 71).

The erect threads of *M. repens* (*Dichosporangium repens* Hauck (70) p. 123, (98) p. 337, (240) p. 51) show little or no longitudinal septation (fig. 36 D), although there is differentiation into short nodal cells (*n*), bearing hairs (*h*) and sporangia (cf. also fig. 36 E, F), and long internodal cells (*i*). Longitudinal division, when it occurs, is usually confined to the nodes.

Sauvageau ((240) p. 78) regards the Mediterranean *M. Protasperococcus* Berth. ((141) p. 65), an unbranched form with sporangia in well-defined annular zones, as the type of a distinct genus, *Protasperococcus*. The little-known *Buffhamia* ((22) p. 307) will perhaps find a place among this series of forms.

Isthmoploea sphaerophora ((68), (96) p. 129, (114), (200) p. 45; *Ectocarpus sphaerophorus* Carm. (95) pl. 126), a small epiphyte with opposite or whorled branches found on diverse Red Algae between tide-levels, is usually classed with the forms under consideration. Longitudinal septation is sometimes confined to the basal parts and varies in extent. The sessile unilocular sporangia generally project in opposite pairs, while the plurilocular sporangia ((111) p. 163) are immersed among the superficial cells (fig. 35 E, *p*); there are no paraphyses. *Isthmoploea* shows points of contact with certain Punctariaceae.

The tendency to form a hollow thallus reaches its extreme in *Asperococcus* ((41), (151) p. 15, (198) p. 53, (199) p. 7, (210), (281) p. 16), in which the plants are usually sack- or bladder-like, with occasional irregular constrictions (fig. 37 A). The wall consists of only a few layers of cells, of which the outermost are the smallest (fig. 37 D). The sori, appearing to the naked eye as dark dots irregularly scattered over the surface (fig. 37 A, *s*), include numerous 2–3-celled assimilators (fig. 37 D, *a*), intermingled with long hairs (*h*) of the customary type. The two kinds of sporangia are sometimes found in the same sorus.

The two commonest species are *A. fistulosus* Hook. (*A. echinatus* Grev. (95) pl. 194) and *A. bullosus* (fig. 37 A; *A. Turneri* Hook. (95) pl. 11), both of which frequently attain to considerable dimensions; the former occurs in tide-pools, while the latter is found in the sublittoral region. The minute *A. scaber* (140) lacks the usual central hollow, the axis being occupied by four large medullary cells (fig. 37 F). In this species (fig. 37 C) plurilocular sporangia have also been found arising directly from the compact prostrate system ((139) p. 376, (140) p. 51). The germlings are of the usual type ((152) p. 42, (239) p. 363; cf. also (283) p. 79). Impoverished forms, which scarcely get beyond the primary filamentous stage (fig. 37 B, E), are not rare.

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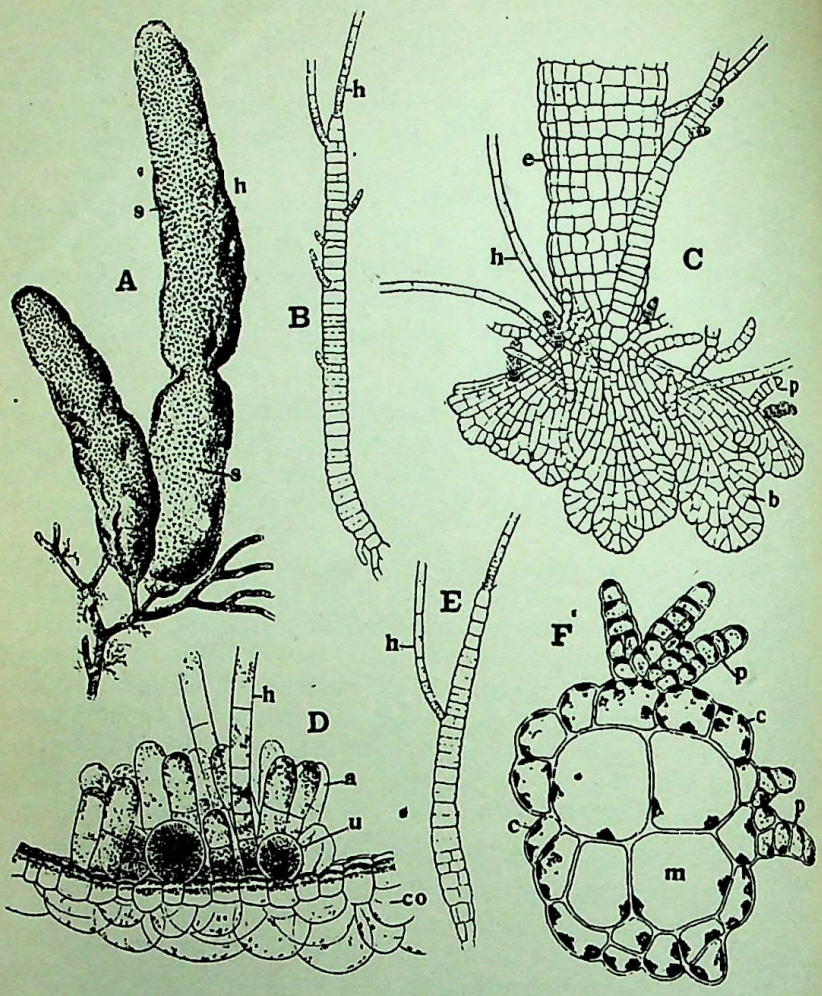

Fig. 37. *Asperococcus*: A, D, *A. bullosus* Lamour.; the rest *A. scaber* Kuck. A, habit; B, E, young stages; C, basal stratum with plurilocular sporangia and base of an adult plant; D, peripheral part of a transverse section, with sorus of unilocular sporangia; F, section of young thallus, with plurilocular sporangia. *a*, assimilator; *b*, basal system; *c*, chromatophore; *co*, cortex; *e*, erect thallus; *h*, hairs; *m*, medulla; *p*, plurilocular and *u*, unilocular sporangium; *s*, sorus. (A after Thuret & Bornet; D after Bornet; the rest after Kuckuck.)

Encoeliaceae (*sensu Oltmanns* (182) p. 66)[1]

Soranthera ulvoidea ((16), (188) p. 19), an epiphyte on Florideae on the western shores of North America, shows many resemblances to *Asperococcus*. The mature plants are hollow, sometimes irregularly lobed, vesicles (fig. 38 B), reaching a diameter of 7 cm. and with a

[1] An altogether artificial assemblage (cf. (232) p. 326), the members of which are grouped differently by others (cf. e.g. (256) p. 522 et seq.).

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wall of several layers of cells (fig. 38 D, *w*); the young plants are solid (fig. 38 A). Attachment is effected by a system of threads, some of which (*e*) are endophytic ((16) p. 485, (147) p. 86; cf. however (10)). The scattered sori (fig. 38 B, *s*) of unilocular sporangia (fig. 38 D, *u*) are interspersed with numerous clavate assimilators (*a*). The sporangia are grouped around a central tuft of hyaline hairs (*h*), commonly situated at the base of a depression. It is this approximation of

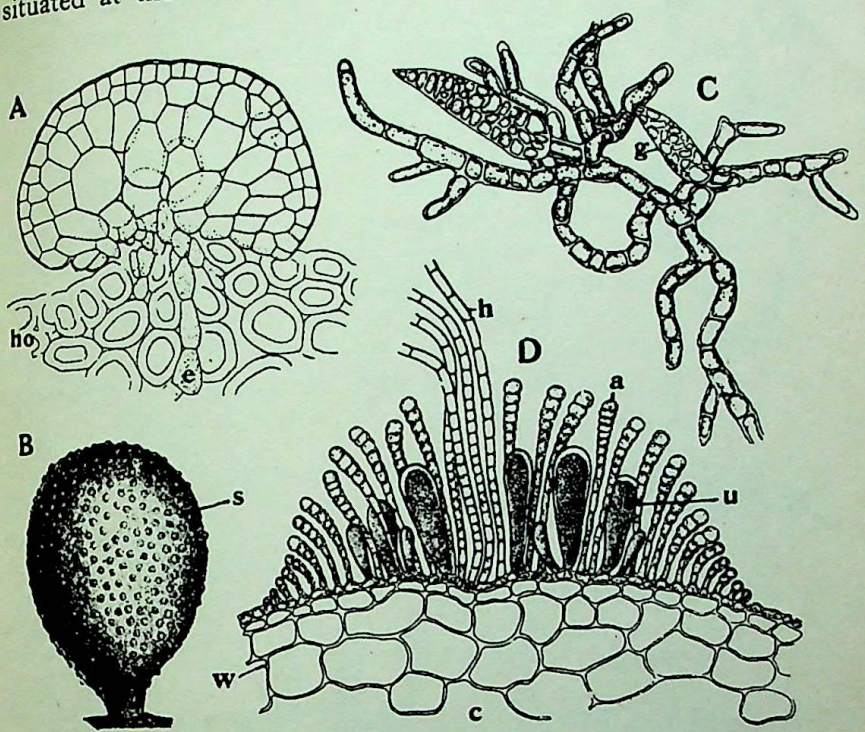

Fig. 38. *Soranthera ulvoidea* Post. & Rupr. A, vertical section of young stage; B, habit of mature plant; C, gametophyte; D, periphery of transverse section, with sorus. *a*, assimilator; *c*, central cavity; *e*, endophytic filaments; *g*, gametangium; *h*, hair; *ho*, host; *s*, sorus; *u*, unilocular sporangium; *w*, wall of vesicle. (A after Kuckuck; B after Kjellman; C after Angst; D after Setchell & Gardner.)

sporangia and hairs that essentially distinguishes the forms now under discussion.

The irregularly lobed and often sinuous vesicles of *Colpomenia sinuosa* (fig. 39 A) are not unlike a *Leathesia* in appearance; older thalli often tear open irregularly. This seaweed is widely distributed in warmer seas, but early in the present century another form, of more delicate texture and less sinuous, became naturalised on the Atlantic shores of Europe (cf. (49), (51), (60), (157), (223), (225) p. 19 and (232), where the earlier literature is summarised). According to Sauvageau ((232) p. 321) this constitutes a distinct variety (var. *peregrina*), agreeing in

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many respects with specimens described from the Pacific coast of North America, whence he believes the European form to have been introduced. Its rapid multiplication has caused considerable damage to the French oyster-beds (221); when filled with gas as a result of

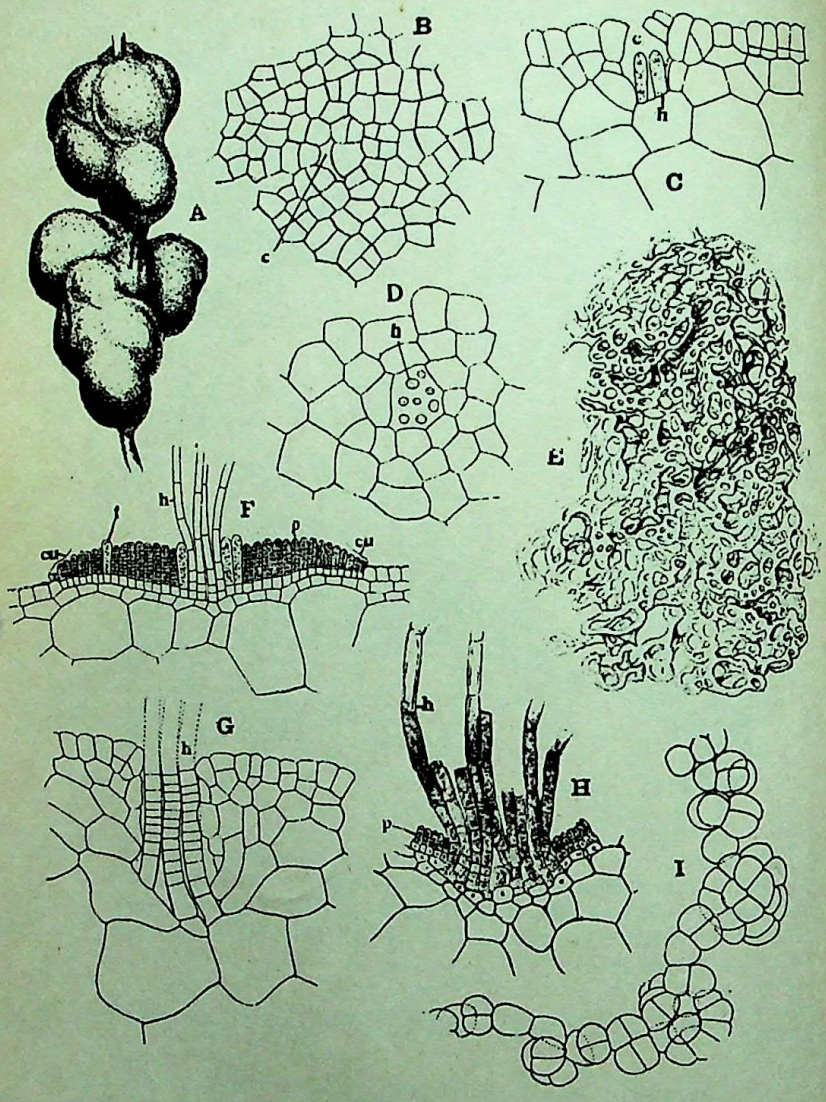

Fig. 39. A–D, F, G, I, *Colpomenia sinuosa* (Roth) Derb. et Sol.; A, habit; B, early development of cryptoblast (*c*) from the surface; C, D, later stage, in transverse section and surface view respectively; F, section of sorus; G, mature cryptoblast in section; I, early development. E, H, *Hydroclathrus cancellatus* Bory; E, part of an older plant; H, section of a sorus. *c*, cryptoblast; *cu*, cuticle; *f*, paraphysis (fucosan-receptacle); *h*, hair; *p*, plurilocular sporangium. (A, E, H after Mitchell; F after Boergesen; the rest after Sauvageau.)

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photosynthesis, the often large thalli lift the young oysters and carry them out to sea (cf. also (44) p. 36).

The mature structure has been described by Mitchell (169), while the accounts of the early development are somewhat conflicting. According to Sauvageau ((232) p. 339) certain cells of the primary creeping filaments divide to form clusters (fig. 39 I), from which, evidently much as in *Soranthera*, the young globular thalli originate. Killian and Werner ((113) p. 90), on the other hand, state that it is cells of the erect threads that divide by radial walls to form the mature thallus. The large central hollow arises as a result of extensive surface-growth effected by repeated crosswise division of the superficial cells ((232) p. 329). *Colpomenia* possesses only plurilocular sporangia which, in the warm-water form, usually constitute dense sori (fig. 39 F), intermingled with unicellular paraphyses (*f*) functioning as fucosan-receptacles; the centre of the sorus is occupied by a tuft of hairs (*h*) arising from an often ill-defined depression. As the sorus develops, the surface-pellicle (cuticle, *cu*) is lifted and ultimately burst. In var. *peregrina* the association of sporangia with the depressions is for the most part fortuitous, most of the sori arising quite independently of them (cf. also (35) p. 262).

According to Mitchell (169) the hairs are superficial outgrowths which become sunk owing to abundant division of the surrounding cells. In the French form (var. *peregrina*), however, they originate ((232) p. 329) from cortical cells surrounding a small intercellular space (fig. 39 C), which at first communicates with the exterior only by a narrow gap between the superficial cells (fig. 39 B, C, *c*). This space arises prior to the development of hairs and enlarges by division of the surrounding cells (cf. fig. 39 G).

Hydroclathrus cancellatus Bory ((169), (255) p. 727, (265) p. 23, (277) p. 110), widely distributed in tropical and subtropical seas, is distinguished by the reticulate perforation of the older thalli (fig. 39 E). According to Boergesen ((32) p. 178) interlocking rhizoids may grow out from the cells bounding some of the narrower perforations. Sporangia (fig. 39 H) seem to occur principally on the younger unperforated individuals, where they cover a large part of the surface.

Another member of this series is *Iyengaria stellata* Boerg. ((36) p. 91; *Rosenvingea stellata* Boerg. (34)), forming extensive communities above low-water mark in tropical India; the thallus is provided with projections which give it a somewhat stellate appearance (cf. also (103), p. 505).

A different habit is shown by *Chnoospora* ((4), (5) p. 170, (17), (35) p. 263, (160) p. 21, (255) p. 728), which is apparently confined to warmer seas (especially the Pacific). Kuckuck ((147) p. 83; cf. also (256) p. 552) evidently intended to refer it to a separate family. The small, dichotomously branched thalli (fig. 40 A) bear numerous prominent tufts of hairs which emerge from often barely indicated depressions (fig. 40 E). The thalli are composed of a number of layers of cells (fig. 40 C) and

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grow by means of a subapical meristem (fig. 40 B, *m*). Plurilocul sporangia form dense sori (fig. 40 D, *p*), often aggregated around t tufts of hairs (*h*). Skottsberg's *Cladochroa* ((261) p. 42), recorded fro the Falkland Islands, has a similar habit and structure, but produc unilocular sporangia. The North Pacific *Myelophycus* ((120), (121) p. 20 (256) p. 527) is at present imperfectly known.

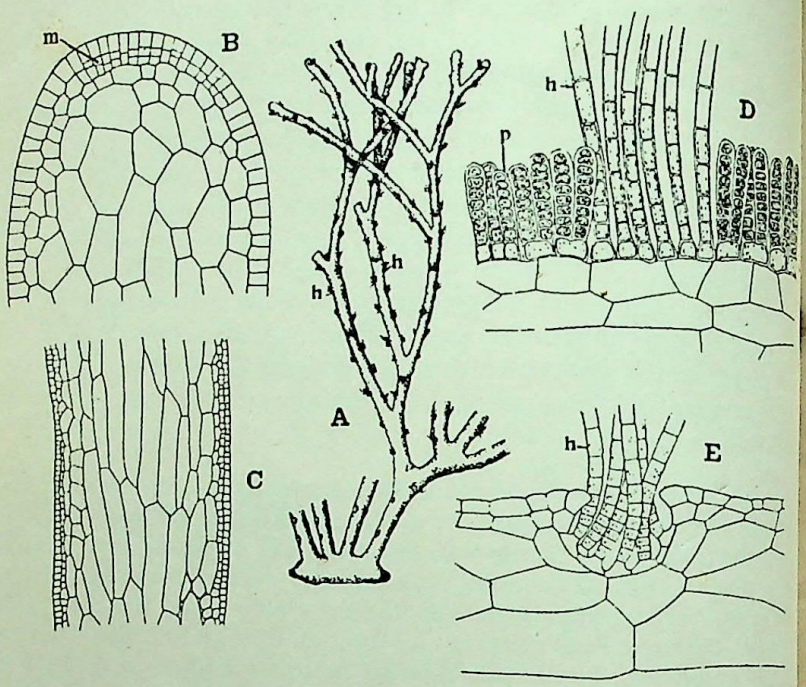

Fig. 40. *Chnoospora*. B, E, *C. obtusangula* (Harv.) Sond., the rest *C. fastigiat* J. Ag. var. *pacifica* J. Ag. A, habit; B, longitudinal section through apex o plant; C, the same, farther back; D, the same, with a sorus; E, the same, with a cryptoblast. *h*, hair; *m*, meristem; *p*, plurilocular sporangium. (B, E after Kuckuck; the rest after Boergesen.)

Dictyosiphonaceae

The polystichous Ectocarpales hitherto considered for the most par exhibit diffuse growth, although in older plants cell-division is some times largely confined to a suprabasal (*Scytosiphon*, (106) p. 113; *Litosiphon*) or subapical position (*Stictyosiphon*, *Chnoospora*). Diverse Dictyosiphonaceae, on the other hand, possess apical growth, effected by a dome-shaped apical cell (fig. 41 F, *ac*), the segments (*s* 1, *s* 2, *s* etc.) of which, as they enlarge, divide longitudinally; Kuckuck and others ((106) p. 100, (147) p. 87, (172) p. 4) have, however, emphasised that some transverse division occurs in the older parts.

There is evidence that, as in Spermatochnaceae (p. 90), the apical growth is secondary and derived from a trichothallic mode of growth.

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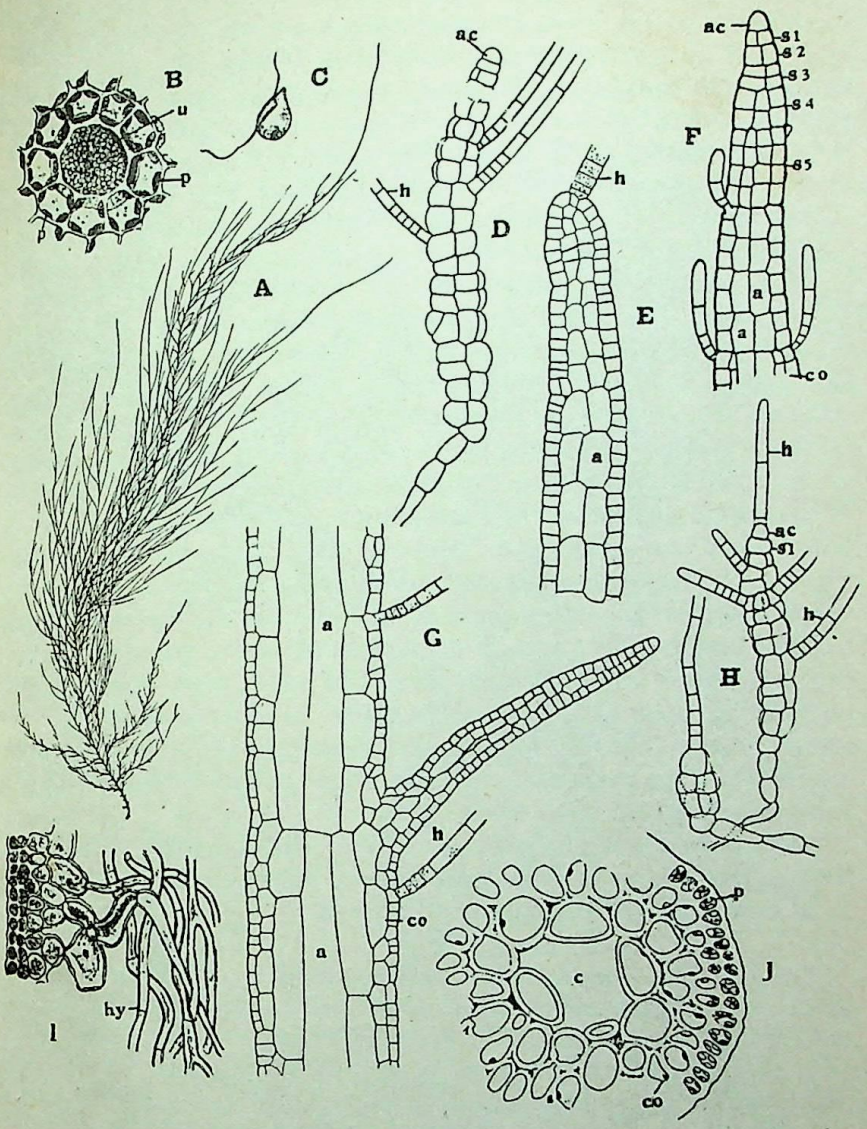

Fig. 41. *Dictyosiphon foeniculaceus* (Huds.) Grev. A, habit; B, small part of thallus from surface, with an embedded sporangium; C, zoospore; D, E, two germlings; F, longitudinal section through apex of thallus; G, ditto through older region; H, early stage of development; I, small part of longitudinal section showing hypha-development; J, transverse section of an almost mature thallus. *a*, axial cells; *ac*, apical cell; *c*, central cavity; *co*, cortex; *h*, hair; *hy*, hyphae; *p*, chromatophore; *s1*, *s2*, etc., segments of apical cell; *u*, unilocular sporangium. (A after Taylor; E after Kuckuck; D, H after Sauvageau; the rest after Murbeck.)

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Thus, young plants of *Dictyosiphon foeniculaceus* bear an apical hair with the usual basal meristem (fig. 41 E, H, *h*). According to Sauvageau ((239) p. 259) this hair arises at an early stage, but it plays no part in the growth of the underlying portion (fig. 41 H), which results from transverse division of the hemispherical cell (*ac*) at its summit. Sooner or later the hair is shed, and the apical cell occupies the actual tip (fig. 41 H, D, *ac*). The apical hair suggests affinity with certain Punctariaceae, with which there are also other points of resemblance. The thalli in this family bear only unilocular sporangia.

The species of *Dictyosiphon* ((11) p. 26, (46), (172), (198) p. 63) are littoral epiphytes or lithophytes. *D. foeniculaceus* ((95) pl. 326), a slender form attaining a length of half a metre (fig. 41 A), is richly branched, while *D. Chordaria* Aresch. shows little ramification. The structure of the mature thallus recalls that of *Litosiphon* or *Stictyosiphon*, although showing rather more differentiation. In the younger parts the axis is occupied by four elongate cells (fig. 41 E, G, *a*) which are surrounded by layers of progressively smaller ones (*co*), the outermost containing discoid chromatophores; some of these grow out into hairs (*h*) of the usual type. Most of the mature thallus is hollow (fig. 41 J), owing to separation of the axial cells which ultimately disorganise, but the upper parts of the branches and the extreme base of the plant remain solid. The peripheral layers originate by tangential division of the surface-cells. The inner cells have large pits on the transverse and longitudinal walls. Hyphae arise chiefly from the peripheral cells (fig. 41 I, *hy*) and mainly in the older parts, often appearing in the basal regions of the larger branches and penetrating from there into the main axes.

The numerous large sporangia usually develop singly ((172) p. 25) from superficial cells, but subsequently become embedded (fig. 41 B, *u*) by division of the surrounding cells.

The alga known as *Gobia baltica* ((23), (198) p. 65; *Cladosiphon balticus* Gobi (80) p. 12, (81)), with a little-branched thallus (fig. 42 B), appears to be a depauperate form of *D. Chordaria* ((59), (162) p. 57, (302)).

In *Scytothamnus* ((6) p. 60, (92) p. 219, (101), (261) p. 33), the species of which occur in the Southern Hemisphere, the apical growth is less well defined. In *S. australis* the tip of the thallus (fig. 42 D) is occupied by a group of apical cells ((79), (147) p. 90, (257) p. 48), while in *S. hirsutus* ((261) p. 34) there appears to be only one. The elements of the central tissue are widely separated by mucilage (fig. 42 D, E, *m*), which is traversed by numerous hyphae. The large sporangia occupy the same position as in *Dictyosiphon* (fig. 42 E, *u*).

Delamarea attenuata (Kjellm.) Rosenv. ((202) p. 865; *Physematoplea attenuata* Kjellm. (118) p. 60), first described from the Arctic but later found at Heligoland ((133) p. 246), is probably a related form. The sporangia are embedded amid numerous unicellular assimilators which arise from the cortical cells.

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Coilodesme ((147) p. 87, (192), (205) p. 160) is commonly referred to Dictyosiphonaceae on account of the mode of arrangement of the sporangia (fig. 42 F, *u*), although Setchell and Gardner ((256) p. 577) place it in a family by itself. The early stages ((147) p. 88) afford no evidence of a distinct apical cell and the growth appears to be largely,

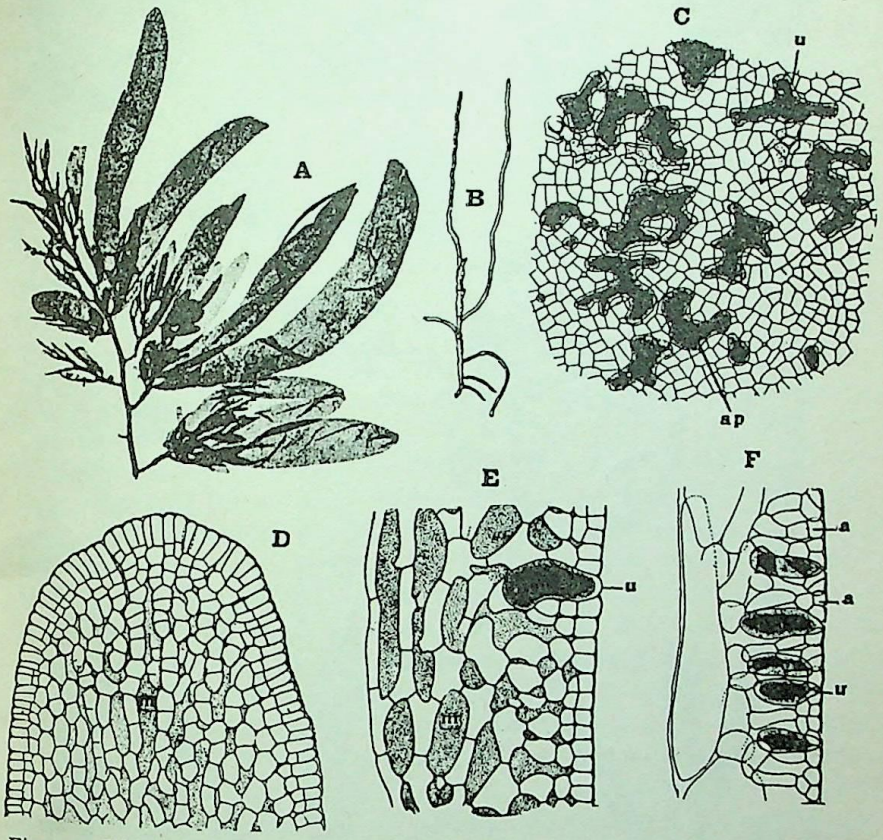

Fig. 42. Diverse Dictyosiphonaceae. A, C, *Coilodesme californica* (Rupr.) Kjellm.; A, group of young plants; C, surface view, with unilocular sporangia. B, *Gobia baltica* (Gobi) Reinke, habit. D, E, *Scytothamnus australis* (J. Ag.) Hook. f. et Harv.; D, longitudinal section through apex; E, the same through the older thallus, with sporangium. F, *Coilodesme bulligera* Strömf., longitudinal section, with sporangia. *a*, assimilators; *ap*, aperture above sporangium; *m*, mucilage; *u*, unilocular sporangium. (A after Setchell & Gardner; B after Gobi; the rest after Kuckuck.)

if not entirely, diffuse. The usually unbranched thalli (fig. 42 A), which often reach a considerable size, include a large cavity which is surrounded by a few layers of cells; the basal stalk remains solid. The sporangia are completely immersed (fig. 42 F, *u*), only a narrow aperture (fig. 42 C, *ap*) remaining above each. This is due to the upgrowth from the peripheral layer of usually 3-celled assimilators (*a*), the outermost cells of which meet to form an almost complete canopy.

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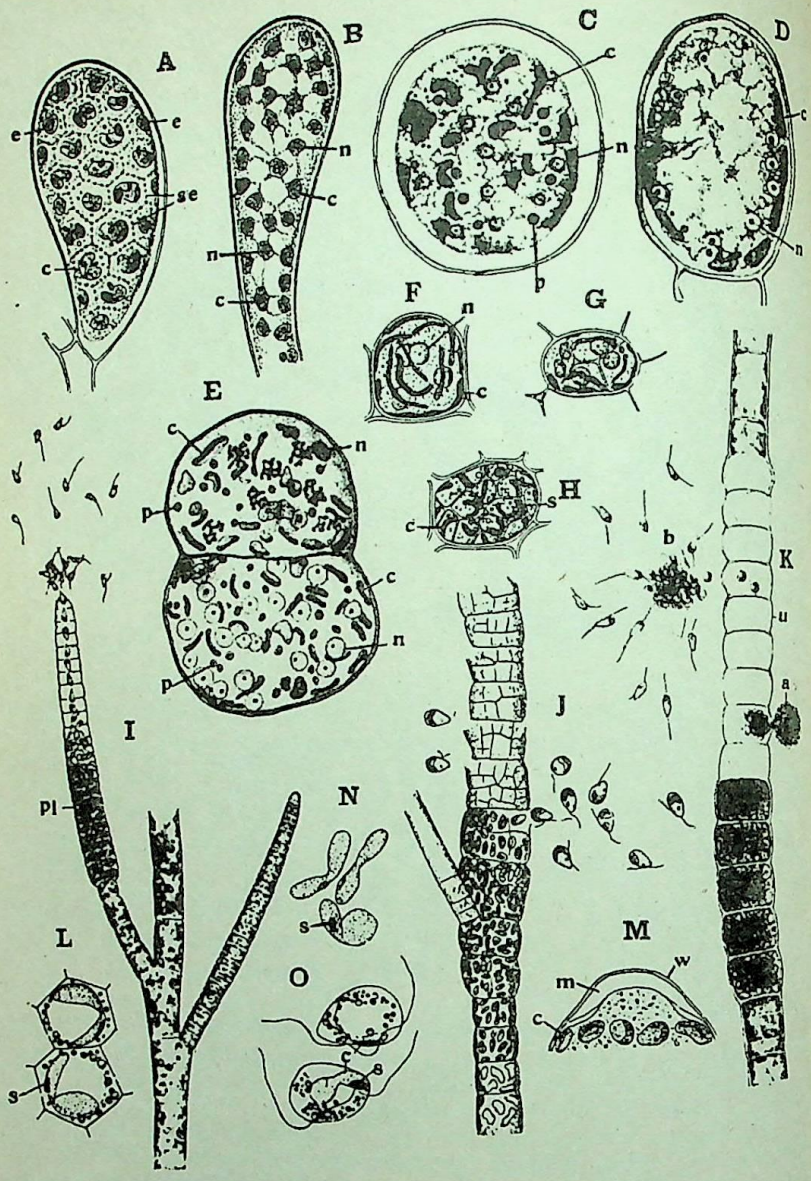

Fig. 43. Development and liberation of swarmers in Ectocarpales. A, B, *Pleurocladia lacustris* A. Br.; A, delimitation of swarmers within the unilocular sporangium; B, earlier stage of development of same. C, D, I, *Ectocarpus siliculosus* (Dillw.) Lyngb.; C, unilocular sporangium in transverse section, with nuclei and chromatophores dispersed; D, the same in longitudinal section, peripheral disposition of chromatophores and nuclei; I, liberation of swarmers from a plurilocular sporangium. E, K, *Pylaiella littoralis* (L.) Kjellm.; E, two unilocular sporangia, in different stages of development; K, liberation of swarmers from unilocular sporangia, *a* and *b* two successive stages. F–H, *Stictyosiphon tortilis* Reinke, successive stages in development of the plurilocular sporangium. J, *S. soriferus* (Reinke) Rosenv., liberation

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In *C. californica* the sporangia are very irregular in shape and vary much in size (fig. 42 C). This species (fig. 42 A) is widely distributed on the Pacific coast of North America, whilst other species (e.g. *C. bulligera*) are subarctic in their distribution ((190) p. 172, (203) p. 61, (256) p. 581).

THE GENERAL FEATURES OF REPRODUCTION

The situation of the uni- and plurilocular sporangia has been fully described in the foregoing pages; they commonly arise in the same position. The details of their development are known only in a few forms ((43) p. 150, (123) p. 98, (126) p. 349, (127) p. 312, (137) p. 360, (145), (167) p. 10, (212)). The young *unilocular sporangium* has a large and conspicuous nucleus and the cytoplasm increases in amount until it completely fills the rudiment; a number of parietal chromatophores are usually present. The first nuclear divisions are no doubt as a rule meiotic (cf. p. 126), although there are certain probable exceptions (p. 137). For a time repeated nuclear division takes place, accompanied by multiplication of the chromatophores; in *Pylaiella* Knight ((126) p. 350) records a long pause after the quadrinucleate condition has been reached.

During the earlier stages of division (fig. 43 B, C) nuclei (*n*) and chromatophores (*c*) are distributed throughout the cytoplasm, but subsequently they assume a peripheral arrangement (fig. 43 D, E), with the chromatophores (*c*) commonly in a profile position perpendicular to the wall; at this stage the chromatophores are often elongate and sometimes more or less wrapped round the nuclei. As the sporangium matures, the contents once again acquire a more even distribution, and this is followed by cleavage of the cytoplasm into uninucleate portions (fig. 43 A), each including one or more chromatophores; according to Kuckuck ((145) p. 164) the initials are sometimes separated by mucilaginous septa. At this stage a brownish red eye-spot (*e*), in intimate contact with a chromatophore (*c*), is recognisable in each initial. Chadefaud ((43) p. 151) states that the chromatophores in the initials of *Mesogloea* become constricted (fig. 43 L, N), the stigma (*s*) arising on the outer surface of one half. According to him the eye-spot in Ectocarpales consists of an oblong colourless highly refractive mass enveloped by pigment. Knight ((127) p. 312), in *Ectocarpus siliculosus*, records a conspicuous granule, regarded as a

of swarmers from plurilocular sporangium. L, N, O, *Mesogloea* sp.; L, two initials from an almost mature unilocular sporangium; N, chromatophores from same; O, zoospores. M, *Cylindrocarpus microscopicus* Crouan, apex of almost mature unilocular sporangium. *c*, chromatophore; *e* and *s*, eye-spot; *m*, mucilage; *n*, nucleus; *p*, pyrenoid; *pl*, plurilocular and *u*, unilocular sporangium; *se*, septum; *w*, cell-wall. (A, B after Klebahn; C–E after Knight; F–H, J after Reinke from Oltmanns; I, K after Thuret; M after Kuckuck; L, N, O after Chadefaud.)

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blepharoplast, during all stages of sporangium-development (cf. also (167) p. 10).

The contents of the sporangium are usually liberated through an apical aperture (lateral in *Pylaiella*, fig. 43 K); prior to dehiscence, the wall in this region develops a mucilaginous middle layer (fig. 43 M, *m*), the swelling of which causes rupture. Most of the contents are usually extruded in a single group (fig. 43 K) enclosed within a thin mucilage-envelope (*a*), but release of the individual swarmers (*b*) takes place almost at once. Extrusion is often violent and affords evidence of a considerable internal pressure (cf. also (280) p. 235). Occasionally small groups of swarmers fail to separate from one another. The cell below the sporangium may grow into the empty cavity and form either a new one or continue as a vegetative thread.

The swarmers (fig. 43 O) are haploid and as a general rule behave as asexual zoospores; they show the characteristic features of the motile cells of Phaeophyceae (p. 40) and contain one or several chromatophores. They are often markedly phototactic ((151) p. 3, (152) p. 11; cf. however (1) p. 329). Certain species (e.g. *Ectocarpus tomentosus* (209), (217) p. 360; *E. granulosus* (145) p. 175; *Pylaiella fulvescens* (37)) produce zoospores of specially large size which often show little motility, apart from amoeboid movement.

After swarming for some time, the zoospores, in some species of *Ectocarpus*, become attached with the help of a sucker-like enlargement formed at the tip of the anterior flagellum ((27) p. 404, (151) p. 10). By the gradual contraction of the latter the body of the swarmer is drawn on to the substratum; this is followed by the withdrawal of the other flagellum, rounding off, and secretion of a membrane, after which immediate germination to form a filament ensues. It is not known whether this method of attachment is frequent, and it seems that the zoospores commonly settle directly on a substratum. In the more specialised Ectocarpales the rounded cell formed from the zoospore (*embryospore*, fig. 47 A) puts out a tubular prolongation (fig. 47 B) into which most or all of the contents pass, after which the prolongation is cut off by a septum (fig. 47 C); it is this cell which divides to produce the prostrate system of the gametophyte (fig. 47 D, E).

The *plurilocular sporangia* are generally more elongate than the unilocular ones; those of *Ectocarpus siliculosus* become progressively shorter as the season advances ((127) p. 310, (132)). As a general rule the rudiment undergoes successive divisions by transverse septa, and the row of flat cells thus produced may constitute the mature sporangium (e.g. *Ascocyclus*, fig. 8 D; many Myrionemataceae, fig. 9 J; *Myriactula*, fig. 16 C). Commonly, however, longitudinal walls appear at a fairly early stage leading to division of the primary compartments into quadrants, and this may be followed by further segmentation (figs. 4 G; 7 A; 8 L) by vertical septa so that as many as 24 chambers

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may be present in the cross-section of the sporangium; the degree of segmentation probably often varies within fairly wide limits in one and the same species. As a result of this regular septation the plurilocular sporangia usually possess cubical compartments of approximately even size (figs. 31 L; 34 E).

In most Ectocarpales septation of the developing plurilocular sporangium seemingly ensues after each nuclear division, in conjunction with division of the chromatophores. In *Lithoderma* ((145) p. 167), however, nuclear division is completed before any formation of septa occurs, while in *Stictyosiphon tortilis* ((145) p. 164, (200) p. 49, (294) p. 130, as *Phloeospora subarticulata* Aresch.) several divisions of the chromatophores and of the nucleus may occur before the first septa are laid down (fig. 43 F–H). As Oltmanns ((182) p. 72) points out, such sporangia in their development show appreciable approximations to the unilocular type. According to Knight ((127) p. 310) the young plurilocular sporangium of *Ectocarpus siliculosus* possesses dense cytoplasmic contents and reduced chromatophores; a probable blepharoplast-granule is recognisable during the later divisions.

Dehiscence of the plurilocular sporangium ((280) p. 234) is commonly at least effected by a single apical aperture (fig. 43 I); the septa between the individual compartments disappear completely (*Stictyosiphon tortilis*) or only the central region is dissolved. The swarmers, produced singly from each compartment, pass out in a slow stream or in a series of bursts ((168) p. 542) through the apical aperture (fig. 43 I), a method of liberation contrasting with that observed in the unilocular sporangium (cf. also (61) p. 218, (280) p. 233). In *Zosterocarpus* ((121) p. 186), *Castagnea*, *Lithoderma*, and certain species of *Ectocarpus*, however, each compartment of the sporangium opens separately to the outside (cf. also fig. 43 J). No septa are formed in conjunction with the later divisions of the plurilocular sporangia of *Heribaudiella* (fig. 10 B), so that each of the primary compartments furnishes a number of swarmers (fig. 10 C); the latter are stated to lack chromatophores in the mature condition ((78) p. 587, (270) p. 908).

As already mentioned, the plurilocular sporangia of Ectocarpales include structures of diverse nature. Those found upon diploid individuals, also bearing unilocular sporangia, produce diploid swarmers which constitute an accessory method of multiplication of the sporophyte. Such diploid accessory swarmers either reproduce the sporophyte direct or give rise for a period to dwarf ectocarpoid stages reproducing by diploid plurilocular sporangia (cf. p. 132). Occasionally they germinate directly within the sporangium ((168) p. 543). The haploid swarmers from the unilocular sporangia produce gametophytes, which are either identical in form with the sporophytes or more usually are represented by minute filamentous stages. The plurilocular sporangia, borne upon the haploid gametophytic stages, are gametangia which form haploid gametes. The zygotes directly or

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indirectly (p. 133) produce the new diploid phase. Although there are diverse exceptions and the full life-cycle has only been followed in a few species, the preceding statement probably applies to many Ectocarpales.

Most members of the order appear to be morphologically isogamous and monoecious ((125) p. 153), although *Ectocarpus siliculosus* is usually dioecious (cf. however (145) p. 157) with distinct male and female strains. Goebel ((82) p. 179) reported an altogether isogamous sexual fusion in *Ectocarpus globifer* Kütz. (as *E. pusillus* Kütz.), but this has never been confirmed, and it is probable that physiological anisogamy is the rule. The sexual process of *E. siliculosus*, first described by Berthold (27) and often since corroborated ((89), (90), (145) p. 156, (181), (216)), clearly demonstrates the sharp degree of differentiation. Despite the morphological identity of the two kinds of gametes, the female move less actively and for a shorter period ((90) p. 128); they come to rest on the illuminated side of the containing vessel, attaching themselves, like the zoospores, by their anterior flagellum. Each such passive female swarmer (fig. 44 B, *f*) becomes surrounded by numerous gametes (*m*) of the opposite sex which, still showing vibrating movements, in part at least fix themselves to the former by their forward flagellum. Soon the anterior flagellum of one of the male gametes contracts (fig. 44 C, D) so that its body is brought into contact with that of the female, after which the two progressively fuse (fig. 44 E–G; cf. also fig. 45 B–F); the remaining male gametes swarm away. This type of clump-formation (1, p. 44) in which each group gives rise to a single zygote is, so far, recorded only in *Ectocarpus*, although not always found there ((29) p. 419). The method of fusion of the gametes just described and illustrated in fig. 44 C–H would, however, appear to be frequent among Ectocarpales (145).

A fusion of morphologically isogamous gametes is also reported *inter alia* for *Ascocyclus* ((229) p. 1578), *Lithoderma* ((145) p. 170; cf. fig. 44 A), *Mesogloea vermiculata* ((187) p. 36), *Phloeospora brachiata* ((167) p. 15), *Asperococcus bullosus* ((129) p. 93), *Punctaria* (286), *Sorocarpus*, and *Heterochordaria* ((1) p. 331), although few details are available. In *Sphaerotrichia divaricata* (*Nemacystus divaricatus* Hygen (104) p. 245) larger female and smaller male gametes are recorded, and the former are stated also to develop apogamously. *Soranthera* ((9) p. 161) is described as having large, dark-coloured, sluggish female gametes and small, transparent, active male gametes, as well as swarmers of an intermediate type; both of the latter can apparently fuse with the female gametes. In neither instance do the published figures afford clear evidence of the existence of more than one type of plurilocular sporangium on the gametophytes (cf. fig. 38 C), and further investigation is needed to establish the true state of affairs.

According to Hartmann ((90) p. 132) the two types of gametes in *Ectocarpus siliculosus* can be distinguished by *intra vitam* staining and

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((91) p. 387) contain specific sexual substances. It is not altogether easy to harmonise this with the occurrence of relative sexuality ((89) p. 463, (90) p. 138, (91) p. 385), i.e. the fusion between two different groups of gametes belonging to the same strain. Hartmann ((90) p. 146) concludes that sex determination in this species is phenotypic.

Several species of *Ectocarpus* (fig. 45) possess more than one kind of plurilocular sporangium, the compartments being of different sizes

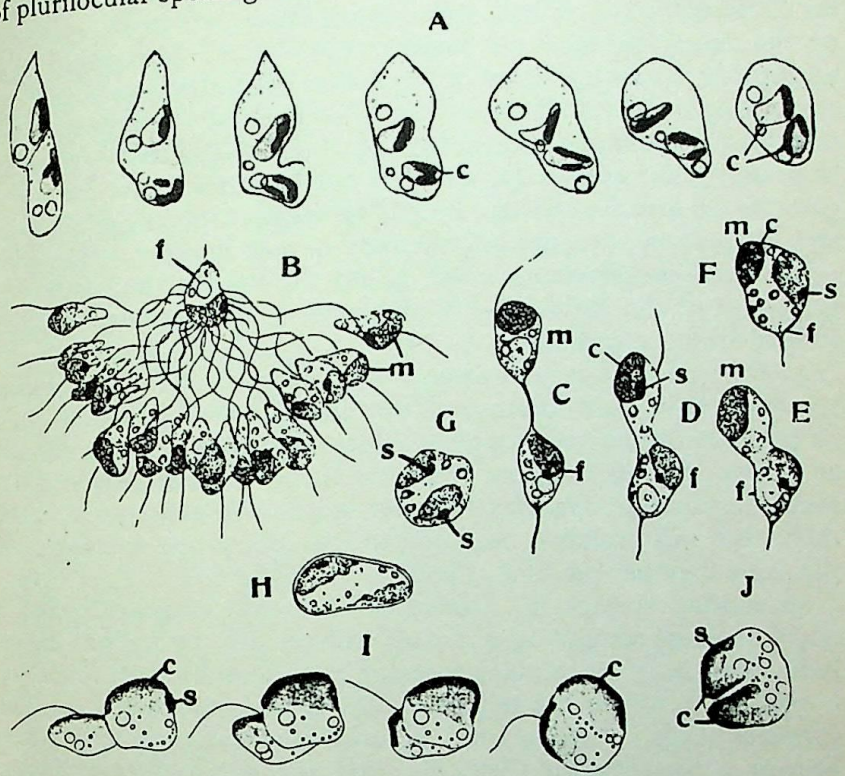

Fig. 44. Sexual fusion. A, *Lithoderma fatiscens* Kuck., progressive stages in fusion of gametes. B–H, *Ectocarpus siliculosus* (Dillw.) Lyngb.; B, clump-formation; C–F, progressive stages in fusion; H, zygote. I, J, *Scytosiphon Lomentaria* (Lyngb.) Ag.; I, fusion; J, zygote. *c*, chromatophore; *f*, female and *m*, male gamete; *s*, eye-spot. (A, I and J after Kuckuck; B–H after Berthold.)

and different types of swarmers being produced. The one kind (meiosporangium) seemingly serves to produce accessory asexual swarmers, while the others (megasporangia and microsporangia) constitute gametangia. Kniep ((125) p. 155), however, regarded the megasporangia as asexual and the meiosporangia as female organs. In view of the marked anisogamy shown by some of these species, they were referred by Batters (21) to a distinct genus *Giffordia*, but such separation is not warranted, since the heterogamous species of *Ectocarpus* are in part closely allied to isogamous ones ((212) p. 265).

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In the rare *E. secundus* ((39), (217) p. 388), in which meiosporangia appear only towards the end of the growing season ((242), (244) p. 51), the female gametangia (fig. 45 A, *ma*) have large compartments containing a number of deep brown chromatophores, while the male (*mi*) have small, pale-coloured, compartments, each with a single minute yellow chromatophore. Sexual fusion ((217) p. 390) occurs between the two kinds of gametes (fig. 45 C–F) after the manner above described for *E. siliculosus*, the female soon coming to rest and being sought out by the males. Apogamous development of the megagametes is not uncommon in the later part of the season when the male gametangia are lacking and, in *E. Padinae* Sauv.[1] ((42) p. 88, (48) p. 371, (218) p. 24, (226)) with similar gametangia (fig. 45 N–P), this is always so, so far as present observations go, and it is not known whether the microgametes are ever functional. In *E. Padinae* meiosporangia (fig. 45 M, *me*), with compartments intermediate in size between those of the micro- and megasporangia, are found throughout the season; the germlings of the meiospores show narrower dimensions than those formed from megaspores.

In the two species just discussed no individuals with unilocular sporangia have been discovered, and the plants so far studied must be presumed to be gametophytes which can propagate apogamously, as well as by means of the swarmers from the meiosporangia. The sexual fusion in *E. secundus*, however, implies the existence of diploid thalli that will probably be found to bear unilocular sporangia, and the same may be true of *E. Padinae*.

In another species, *E. Mitchellae* Harv. (*E. virescens* Thur.), in which megasporangia and meiosporangia are borne on distinct individuals (213), unilocular sporangia have recently been found ((36) p. 75, (244) p. 67) on plants bearing also meiosporangia (fig. 45 G–I). Cultures of the swarmers from the unilocular sporangia afford plants bearing megasporangia (fig. 45 J, *ma*) and microsporangia (fig. 45 K, L, *mi*). The swarmers produced by the former show a tendency to loss of movement ((218) p. 33), while those of the latter are colourless, save for the eye-spot. No fusion of the two kinds of swarmers has been observed, but the megagametes can give rise to further generations bearing the same two types of reproductive organs. It is probable, however, that sexual fusion occurs in nature (cf. (125) p. 144) and that the zygotes develop into the plants bearing the unilocular sporangia which are otherwise inexplicable. Svedelius (269) has shown that plants bearing megasporangia or meiosporangia both possess the same number of chromosomes, which suggests a formation of meiosporangia also on the gametophyte (cf. *E. secundus* and *E. Padinae*). Those on the plant with unilocular sporangia can hardly be other than diploid.

[1] As regards the possible relation of this species to *Acinetospora pusilla*, see (226) and (236) p. 67.

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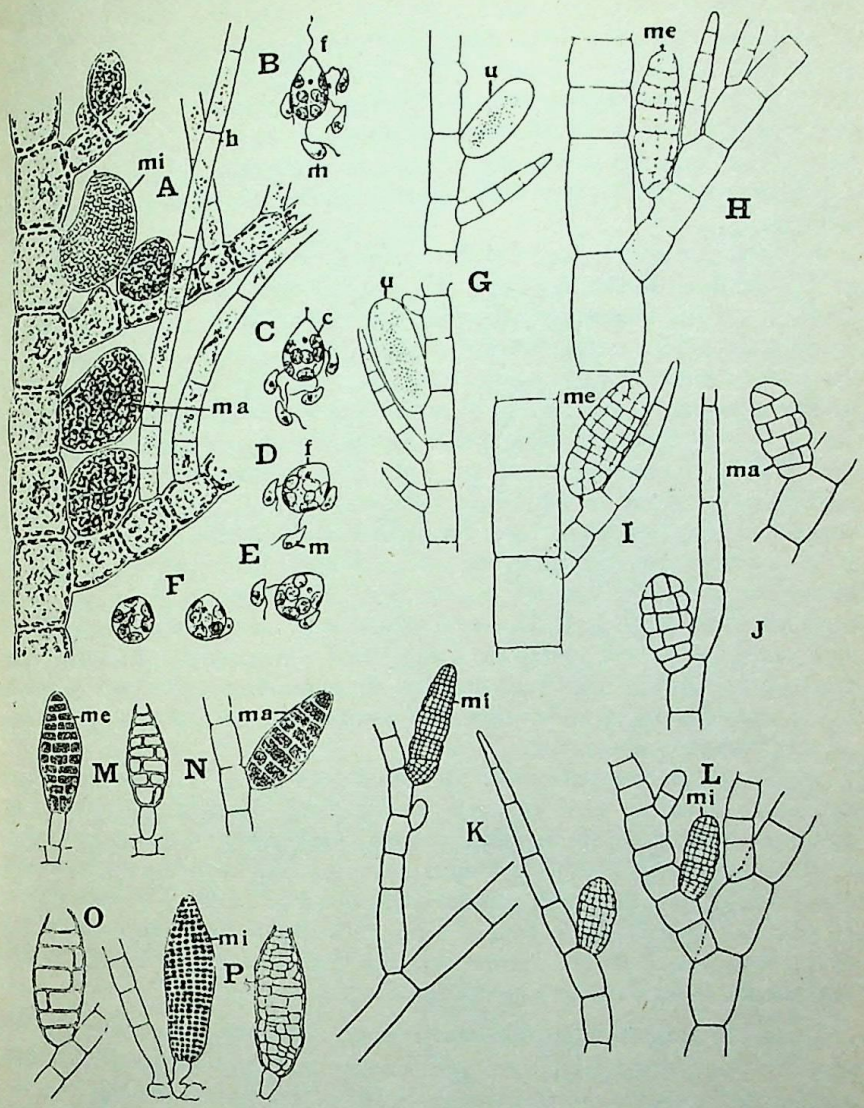

Fig. 45. Heterogamy in *Ectocarpus* (after Sauvageau). A–F, *E. secundus* Kütz.; A, part of thread, with the two kinds of gametangia (mega- and microsporangia); B–F, sexual fusion. G–L, *E. Mitchellae* Harv.; G, thread with unilocular sporangia; H, I, the same, with meiosporangia; J, the same, with megasporangia; K, L, the same, with microsporangia. M–P, *E. Padinae* Sauv.; M, meiosporangia; N, O, macrosporangia; P, microsporangia. *c*, chromatophore; *f*, female and *m*, male gamete; *h*, hair; *ma*, macrosporangium; *me*, meiosporangium; *mi*, microsporangium; *u*, unilocular sporangium.

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Two kinds of plurilocular sporangia[1] have also been recorded in *E. Lebelii* Crouan ((39) p. 355, (218) p. 5, (281) p. 24), the one with very small compartments producing swarmers like the male gametes of *E. secundus*, the other with deep brown compartments. No fusion of the swarmers has been observed, and it remains doubtful whether those of the second kind represent meiosporangia or megasporangia. Askenasy ((15) p. 8) also describes two types of plurilocular sporangia in *E. indicus* Sond. The large-chambered plurilocular sporangia recorded in *E. confervoides* are, according to Sauvageau (215), the result of the attack of a parasite.

Plurilocular sporangia of different sizes are not, however, confined to *Ectocarpus*. Howe ((102) p. 48) records two kinds in *Streblonema Cokeri*. In *Myrionema strangulans* Sauvageau ((220) p. 218) describes some with large compartments regarded as megasporangia and other rarer ones with compartments of about half the size, interpreted as meiosporangia; Kylin ((153) p. 8), who observed only those of the former type, regards them as comparable to the meiosporangia of *Ectocarpus Mitchellae*. Karsakoff ((112) p. 435) also recorded in *Myriotrichia filiformis* two kinds of sporangia, the swarmers of which were stated to copulate. This has never been confirmed and, in view of what is known of the sexual reproduction of allied forms, the reported fusion of swarmers is improbable (cf. (145) p. 175, (152) p. 34, (217) pp. 359, 395; see however (125) p. 151). Several kinds of plurilocular sporangia have also recently been reported in *Colpomenia sinuosa* (148). In spring the plants are stated to bear male and female gametangia, the male gametes being considerably smaller than the female and devoid of a chromatophore; fusion is described.

In *Giraudya sphacelarioides* Berthold ((27) p. 408) observed megasporangia forming sori on the assimilatory threads and liberating swarmers with several chromatophores, while recent workers have seen only meiosporangia with swarmers having a single chromatophore and occurring in the three types of sori described on p. 71. The only record of sexuality in this alga is that of Goebel (82), who describes conjugation of the swarmers from the megasporangia. Recent workers have generally regarded this as a misinterpretation ((147) p. 32).

Incipient oogamy, similar to that of *Ectocarpus secundus*, is also seen in *Nemoderma* ((144) p. 122), where the male and female gametangia are borne laterally on the upper parts of the erect threads (fig. 46 A, *ma*, *mi*), while the intercalary unilocular sporangia (fig. 46 D, *u*) occur on distinct individuals. The gametes are liberated singly from the compartments of the gametangia (fig. 46 B). The large female swarmers (fig. 46 E, *f*), which become attached by the anterior flagellum, are sought out by the small male swarmers (*m*) which lack a chromatophore, although possessed of a distinct eye-spot (*s*). The female gametes can also develop apogamously. The sexual cells ripen fortnightly ((144) p. 144) and are liberated in the interval between two successive spring tides (cf. *Dictyota*, p. 316).

[1] See also the data in (125) p. 143.

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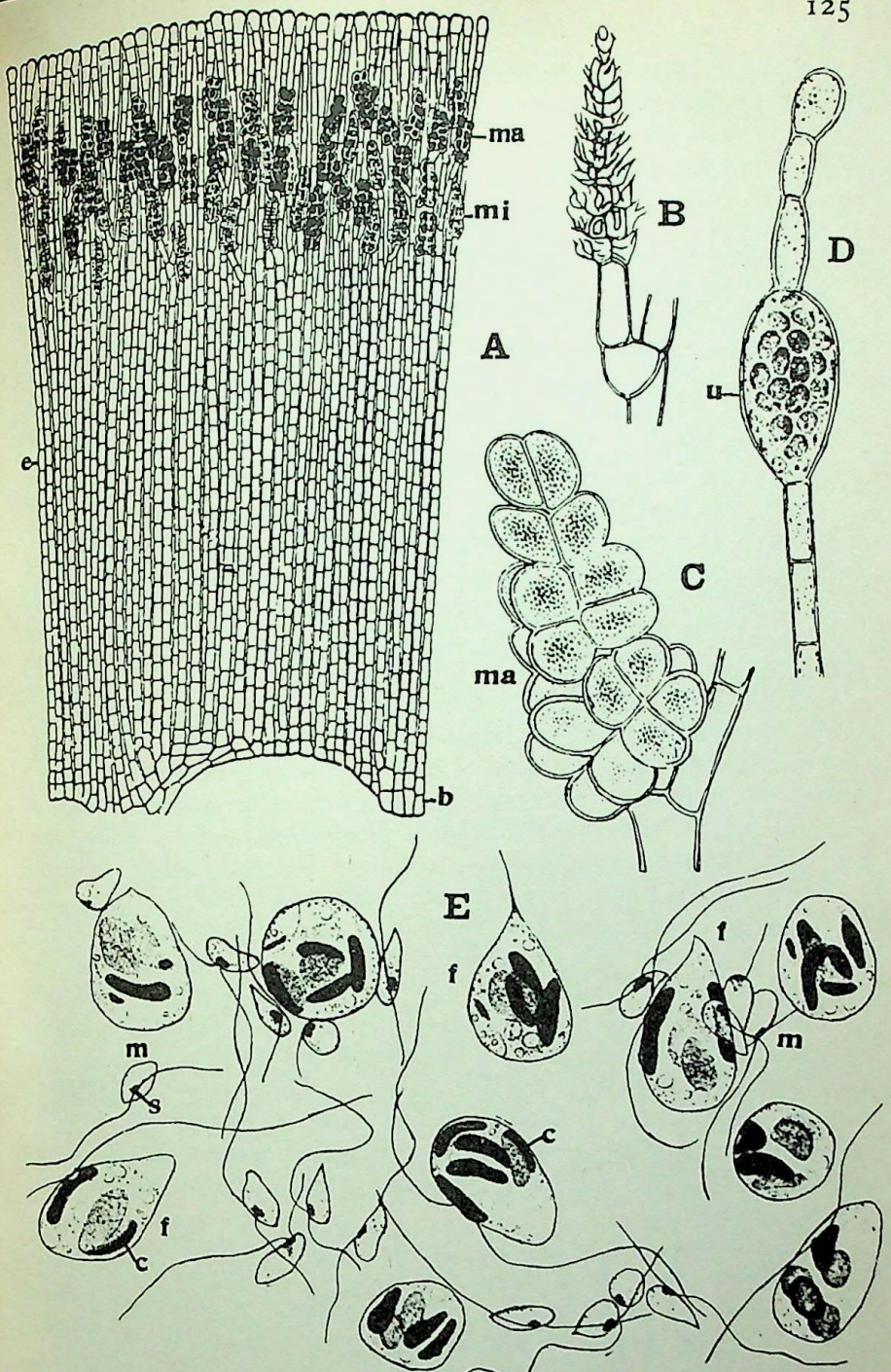

Fig. 46. *Nemoderma tingitana* Schousboe (after Kuckuck). A, vertical section of crust showing the position of the sex organs; B, dehisced male gametangium; C, female gametangium; D, erect thread, with intercalary sporangium; E, sexual fusion. *b*, basal system; *c*, chromatophore; *e*, erect system; *f*, female and *m*, male gamete; *ma*, female and *mi*, male gametangia; *s*, stigma; *u*, unilocular sporangium.

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Although some Ectocarpales thus attain to an advanced state of anisogamy, true oogamy does not appear to have evolved in this order.

THE LIFE-CYCLE IN THE ECTOCARPALES

Of the two main types of reproductive organs met with in Ectocarpales, the unilocular sporangia appear, almost without exception, to constitute asexual organs which produce zoospores germinating without fusion to form a potential gametophyte. The first nuclear divisions in the unilocular sporangium have been shown to bring about reduction in diverse Ectocarpales, a fact first demonstrated by Knight ((126) p. 350) in *Pylaiella littoralis* (cf. also (151) p. 9) and confirmed by Dammann ((56) p. 9). While there are probably a number of instances in which meiosis is suppressed (p. 137), there is little evidence that reduction can occur at any other stage in the life-cycle.[1] Unless there is proof to the contrary, therefore, the swarmers formed from unilocular sporangia must be regarded as haploid, and the plants bearing such sporangia as diploid and sporophytic (cf. (152) p. 75, (269) p. 301).

On the other hand the motile elements produced in the plurilocular sporangia probably always have the same chromosome-number as the parent plant. Where such sporangia occur on plants also bearing the unilocular type, the resulting swarmers are no doubt normally diploid and constitute merely a means of accessory propagation of the sporophyte. When plurilocular sporangia occur on what is known to be a haploid phase, they are invariably unaccompanied by unilocular sporangia and have in diverse instances been shown to liberate gametes which fuse to form a zygote producing a new diploid phase. The frequent absence of observed fusion cannot be taken as definite proof that the swarmers in question lack sexuality, since the artificial environment of a laboratory is only too likely to create conditions inimical to the occurrence of sexual fusion; this is moreover clearly dependent on outside factors, as shown by various data in the literature (cf. (90) p. 135, (125) pp. 146, 154). The usual close resemblance between the accessory plurilocular sporangia on diploid individuals and those which function as gametangia on the haploid phases, is one of the reasons why the life-cycle of Ectocarpales so long remained obscure.

The investigations of the last two decades have made it clear that the complete life-cycle in this order involves an alternation between (*a*) a diploid individual bearing asexual (unilocular) sporangia (often accompanied by accessory plurilocular sporangia) and (*b*) a haploid individual bearing plurilocular sporangia which function as gametangia. In the simple filamentous Ectocarpaceae the two generations

[1] Knight ((126) p. 355), however, states that on certain diploid plants of *Pylaiella* the last divisions of the plurilocular sporangia showed the haploid number of chromosomes.

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are essentially alike and the alternation is isomorphic. The elaboration, which the thallus has undergone in the more advanced members of the Ectocarpales, has in a few instances affected both sporophyte and gametophyte, so that the alternation is likewise isomorphic (*Nemoderma*, *Heterochordaria abietina*, p. 130). More usually, however, only the sporophyte has been elaborated, whilst the gametophyte remains a small ectocarpoid or streblonemoid structure (fig. 47 G, H) so that alternation has become heteromorphic. Fundamentally, however, wherever alternation occurs in Ectocarpales it is derived from a state with two identical generations (300), i.e., using the term in its old sense, alternation throughout the Ectocarpales is originally homologous (cf. (128) p. 29). In considering this interpretation it must be borne in mind that the complex sporophyte of the Ectocarpales practically always originates from an erect thread or threads of an heterotrichous filament, essentially—though not in detail—resembling the simple filamentous gametophyte (cf. e.g. fig. 31 A, H, with fig. 47 F, G, H). The sporophyte does not ordinarily become fertile until the mature structure has been attained, whereas the gametophyte, in forms with heteromorphic alternation, forms reproductive organs while still in a filamentous condition. Precocious fertility on the part of the sporophyte is, however, frequent (cf. pp. 97, 107; (299); figs. 36 H; 37 C).

(*a*) Forms with Isomorphic Alternation

Two practically identical generations are probably not uncommon in *Ectocarpus* and its allies. In *E. siliculosus* Berthold showed that the plants found at Naples during spring reproduce sexually by means of gametes liberated from the plurilocular sporangia, the only kind of reproductive organs present. The fate of the zygote was not clearly established, although some evidence was produced ((27) p. 412) that it developed into a small plant bearing uni- and plurilocular sporangia. Sexual reproduction in *E. siliculosus* at Naples has since been studied by diverse investigators ((89, 127, 145, 181, 193, 216); cf. also (217) p. 365) and Knight ((127) p. 318) showed that the plants producing gametes are haploid. Berthold's conclusions as regards the sporophyte have also been confirmed ((72) p. 4, (250) p. 91); at Naples it is a winter-form, considerably smaller than the gametophyte and bearing, apart from unilocular, accessory plurilocular sporangia.

A similar alternation has been established in *E. siliculosus* by Föyn ((72) p. 6) on the west coast of Norway and by Papenfuss (185) at Woods Hole in North America; both record haploid plants with plurilocular sporangia only and diploid plants with pluri- and unilocular sporangia, either on the same or on distinct individuals. The diploid plants at Woods Hole, however, are more robust than the haploid ones, possessing bigger cells and considerably larger plurilocular

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sporangia. It would thus seem that in northern waters, by contrast to the condition obtaining at Naples, the diploid plant of the species under discussion is more vigorous than the haploid one. This is in harmony with the fact that Knight ((127) p. 322) in the Isle of Man found only diploid plants, while Kylin ((152) p. 16; cf. also (162) p. 31, (168) p. 547), on the west coast of Sweden, records plants (assumed to be diploid) with mainly plurilocular sporangia that liberate asexual swarmers. The occurrence of reduction in the unilocular sporangium of *E. siliculosus*, first established by Knight ((127) p. 314), has since been confirmed on material from diverse regions ((184, 185, 250); cf. also (168) p. 545).

While, therefore, *Ectocarpus siliculosus* in various localities exhibits a distinct alternation with varying preponderance of sporophyte or gametophyte, there is some evidence that yet another type of life-cycle may occur. Knight ((127) p. 316), in her British material, records fusion of the swarmers from the unilocular sporangia,[1] and a similar state of affairs has been reported from the Adriatic ((250) p. 85). Knight's data are perhaps not altogether convincing ((152) p. 19, (185) p. 423), but analogous observations since published (cf. p. 131) strengthen the indications that such a behaviour on the part of these normally asexual swarmers is possible. I am inclined to interpret the phenomenon as an instance of extreme reduction, since under these circumstances the gametophyte is completely eliminated and the asexual cells that normally produce it themselves behave straight away as gametes (cf. *Saccorhiza*, p. 251 and (300)). Such curtailment of the life-cycle can, however, no longer be regarded as characteristic of northern latitudes (cf. (127) p. 321) in view of its occurrence also in the Adriatic.

All who have studied the sexual reproduction of *E. siliculosus* have reported that a certain percentage of the gametes fail to fuse. Such gametes (apparently mainly the female ones, cf. however ((184)) can develop apogamously with the production of further plants bearing plurilocular sporangia only ((27) p. 412), and in this way accessory reproduction of the haploid phase takes place. In the normal life-cycle of the species under discussion, therefore, either phase can propagate itself indefinitely, the diploid phase with the help of the accessory swarmers from the plurilocular sporangia, the haploid phase with the help of apogamous gametes.

The successive individuals, which may thus for long periods perpetuate the diploid or haploid phase as the case may be, do not in *Ectocarpus* ordinarily appear to display any essential differences from the normal adult thallus. Instances are, however, on record in which both the accessory sporophytic phases derived from the swarmers of the plurilocular sporangia and the gametophytic phases derived from

[1] According to Knight ((127) p. 321) this is also true of certain other species of *Ectocarpus* in British waters.

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the swarmers of the unilocular sporangia, show simplification as compared with the adult thallus. Thus, in *E. tomentosus* (237) such stages are described as simple ectocarpoid structures, showing nothing of the fasciculate character typical of the adult plant; they are also distinguished by the hairs which they bear.

There are indications that other species of *Ectocarpus* exhibit an analogous life-cycle. Thus, according to Sauvageau ((218) p. 66, (244) p. 23), *E. Hincksiae* possesses two types of individuals, the one bearing unilocular, the other plurilocular sporangia; in either type plurilocular sporangia may also occur on the prostrate system. The individuals with plurilocular sporangia only are invariably epiphytic on *Saccorhiza*. The lack of viability of the swarmers from the plurilocular sporangia on the erect filaments is regarded as a possible indication of their sexual nature, although fusion has not been observed. The scarcity of plants of *E. Hincksiae* with unilocular sporangia may be due to their being winter-forms[1] or to their growth in deeper water. The reproduction of *E. Mitchellae* (p. 122) also furnishes evidence of isomorphic alternation.

Such a life-cycle evidently also occurs in *Pylaiella*. The individuals of the true *P. littoralis* on the coasts of Scandinavia for the most part bear either uni- or plurilocular sporangia ((154) p. 3, (160) p. 44), the diploid ones being in general larger than the haploid and showing certain other differences ((152) p. 10). In Britain Knight ((127) p. 322) records plurilocular sporangia also on the diploid individuals, while haploid plants are very rare (cf. *Ectocarpus siliculosus*). Kylin ((152) p. 5) finds diploid plants all the year round on *Ascophyllum* (more rarely on *Fucus*), while the haploid ones, occurring on *Sertularia* or on *Ceramium rubrum* epiphytic on *Ascophyllum*, appear in spring and disappear by midsummer. In the Isle of Man (126) the haploid phases are found in spring and, like the diploid ones during early summer, occur on *Ascophyllum*, while later in the season the diploid phase spreads to species of *Fucus*. A seasonal alternation between a diploid spring phase and a probable autumnal haploid one is also implied by the observations of Johnson and York ((107) p. 29).

Fusion of the swarmers from the gametangia on the haploid phases has been observed ((126) p. 354, (152) p. 14), although apogamy is also recorded. Both Knight ((126) p. 353) and Kylin ((152) p. 11) have in cultures grown well-developed gametophytes bearing plurilocular sporangia from the zoospores of the unilocular sporangia of the diploid individuals. The former ((127) p. 322) also records fusion of zoospores, although this was not observed by either Dammann or Kylin (cf. (152) p. 13). In view of the scarcity of haploid plants in the Isle of Man, *Pylaiella littoralis* may display the same tendency as *Ectocarpus siliculosus* towards an elimination of the gametophyte.

Dammann's record ((56) p. 8) of unilocular sporangia on the haploid individuals of *Pylaiella*, the only instance of the kind so far reported, is believed by Kylin ((154) p. 6) to be due to confusion between the two species of *Pylaiella* (p. 55). In *P. rupincola* only individuals with

[1] Cf. also *E. simplex* ((244) p. 92).

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unilocular (and occasional plurilocular) sporangia are known (cf. also (162) p. 33), and the swarmers of the former produce new individuals with unilocular sporangia. This can only be explained by the supposition that there is here no reduction in the unilocular sporangium.

Data in the literature also support the existence of isomorphic alternation in *Sorocarpus* ((154) p. 20, (272)),[1] *Geminocarpus geminatus* (Hook. et Harv.) Skottsb. ((261) p. 9), and *Strepsithalia* ((214) p. 59). Sexuality on the part of the swarmers from the plurilocular sporangia has, however, only been demonstrated in *Sorocarpus* (1).

Among the more specialised Ectocarpales isomorphic alternation appears to be rare, although it probably occurs in *Nemoderma* (p. 124), *Lithoderma* ((145), (151) p. 41; fig. 12), and possibly other Myrionemataceae.[2] It must be noted, however, that neither in *Lithoderma fatiscens* Kuck., nor in *Nemoderma* (144), has a mature plant with unilocular sporangia been grown from the zygote, nor are there at present any cytological data. Apogamy has been observed in both genera.

Another probable instance of isomorphic alternation is furnished by *Heterochordaria abietina* in which uni- and plurilocular sporangia occur on distinct individuals ((256) p. 550). Since heteromorphic alternation obtains in diverse Mesogloeaceae (cf. below), the isomorphic life-cycle of *Heterochordaria* would remove it from that family. Reduction in the unilocular sporangium (3) has been established and, according to Abe (1), the swarmers of the plurilocular sporangia are gametes; there is strict dioecism, the female swarmers being slightly larger and alone capable of apogamous development. Abe (2) also describes a fusion of swarmers from the unilocular sporangia, usually from those of different individuals.

(*b*) Forms with Heteromorphic Alternation

Heteromorphic alternation is definitely established for members of six families of Ectocarpales. These are: Mesogloeaceae (*Castagnea virescens* (187); *Mesogloea vermiculata* (130) p. 113, (152), (187); *Sphaerotrichia divaricata* (104)); Spermatochnaceae (*Spermatochnus paradoxus* (186); *Stilophora rhizodes* (152)); Punctariaceae (*Phloeospora brachiata* (167)); Asperococcaceae (*Asperococcus bullosus* (129); *A. fistulosus* (130) p. 109);[3] Encoeliaceae (*Soranthera ulvoidea* (9, 10)); and Dictyosiphonaceae (*Dictyosiphon foeniculaceus* (224, 239)). In all instances the gametophyte is a minute filamentous plant (figs. 19 G; 38 C; 47 G, H, I, O), with the general characteristics of a small *Ectocarpus* or

[1] The observations of Abe ((1) p. 334) on *Sorocarpus uvaeformis* require confirmation.

[2] Cf. *Ralfsia clavata* ((153) p. 17).

[3] The inclusion of *A. fistulosus* is based on the statements in the work cited, although in a later paper (129) reference is only made to the fusion of swarmers from the unilocular sporangia (cf. below); in view of the data furnished by Kylin ((153) p. 13) it can hardly be doubted that there is normal alternation.

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similar form. The occurrence of reduction in the unilocular sporangium has been established in *Castagnea virescens*, *Mesogloea vermiculata*, *Myriogloea Sciurus* ((187) p. 30), *Spermatochnus paradoxus*, *Phloeospora brachiata*, and *Asperococcus bullosus*.

Plurilocular sporangia do not occur frequently on the diploid individuals of the species listed above, being recorded only in *Castagnea virescens* ((187) p. 17; cf. however (155) p. 31), *Spermatochnus paradoxus* ((246) p. 122), *Stilophora rhizodes* (280), *Phloeospora brachiata*, and *Asperococcus bullosus* ((152) p. 39); even in these, moreover, individuals with unilocular sporangia only are often reported. Among the more advanced Ectocarpales there is thus a tendency to eliminate, either entirely or for the most part, the accessory reproduction by diploid swarmers from plurilocular sporangia which is so frequent among the less specialised members. In this respect the Ectocarpales show a definite evolutionary trend in the direction of the higher Phaeophyceae where such accessory reproduction of the diploid phase does not occur.

Among the species cited above the full life-cycle has only been established in *Asperococcus bullosus* and *Phloeospora brachiata*, but the available data suffice to indicate that the general outline is the same in the other species. The lacunae concern particularly the observation of sexual fusion and the development of a new sporophyte from the zygote. The type of alternation under consideration was first demonstrated in *Dictyosiphon* by Sauvageau (224).

Diverse records in the literature indicate the possibility of occasional fusion of the swarmers from the unilocular sporangia among more advanced Ectocarpales. This was first reported by Areschoug ((11) p. 27) in *Dictyosiphon hippuroides*, although it remains doubtful whether this was a true instance of fusion ((125) p. 138, (224)). Knight ((127) p. 317) records such fusion in *Asperococcus fistulosus* (cf. also (128) p. 23, (139) p. 109), *Myriotrichia clavaeformis*, and *Punctaria plantaginea*, while Hygen ((104) p. 257) assumes its occurrence in *Sphaerotrichia divaricata*. There are, therefore, data supporting the existence of a tendency towards the elimination of the gametophyte in these advanced types, similar to that noted in Ectocarpaceae (p. 128).

Evidence of the occurrence of heteromorphic alternation is available for diverse Ectocarpales in addition to those listed above. In many of these the macroscopic plant bears both uni- and plurilocular sporangia and, although one or other type usually predominates at a certain stage of the life of the individual, there is generally a longer or shorter period of overlap. The unilocular sporangia may be formed before the plurilocular ones (*Leathesia difformis* (152) p. 64, (230)), but more usually the sequence is reversed (e.g. *Stilophora adriatica* (240) p. 144; *Punctaria latifolia* (239) p. 341; *Myrionema strangulans* (153) p. 5; *Litosiphon pusillus* (239) p. 362, (244) p. 2; *Myriotrichia repens* (241); *Protasperococcus myriotrichiformis* (141) p. 67, (240) p. 80). In certain

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instances the two kinds of sporangia tend to occur on distinct individuals which, in *Asperococcus* for example, may show differences in size (cf. (149) p. 78, (151) p. 15, (210)). In general the swarmers from the two types of organs are alike, but in *Litosiphon pusillus* ((239) p. 356) and *Spermatochnus* ((246) p. 128) those from the plurilocular sporangia are described as being markedly larger and exhibiting a less rapid movement.[1]

There can be little doubt that in all the Ectocarpales now under consideration the ordinary plant is diploid and that the swarmers produced in its plurilocular sporangia are accessory and bring about multiplication of the sporophyte before the unilocular sporangia appear. With few exceptions these macroscopic thalli are non-perennial structures, only found for a few months, although the time of their appearance varies in different geographical regions. The restricted period of occurrence is particularly evident in those genera which possess a large thallus, where presence or absence is easily established. The manner in which such forms survived during the period of absence of the macroscopic plant was long a mystery, since no definite resting stages have ever been observed in the life-cycle of Ectocarpales or for the matter of that in any seaweed. Sauvageau (238,243) was the first to elucidate this point (cf. also (193)). He provided evidence that, during the period of absence, these forms persist as minute and largely prostrate filamentous stages, arising from the swarmers either of the uni- or plurilocular sporangia of the macroscopic plant. These germlings are sometimes sterile, but more usually they bear plurilocular sporangia (fig. 47 M, *p*), the swarmers of which can produce several successive generations of such plants.

Sauvageau calls the macroscopic stage the delophycean and the microscopic ephemeral one the adelophycean. The latter sometimes shows a curious dimorphism, some of the plants being discoid or myrionemoid in form, whilst others are streblonemoid ((228), (229), (233) p. 417, (238) p. 267, (239) p. 404), a phenomenon referred to by Sauvageau as heteroblasty. Kylin ((152) p. 58) is of the opinion that the difference results from the degree of rapidity with which the swarmer settles on the substratum (cf. however (301)). According to Knight ((128) p. 26) the alternation between the macro- and microscopic phases may be related to the availability of nitrates and phosphates.

Sauvageau distinguishes three different categories among these filamentous stages. When the swarmers which they produce exhibit sexual fusion, he speaks of the parent-structures as *prothalli*. When there is no evidence of sexuality on the part of the swarmers, the filamentous stages—whether derived from pluri- or unilocular sporangia—are designated *plethysmothalli*. Sometimes such stages directly produce a new macroscopic plant (figs. 34 C; 47 P) and are then termed *protonemata*; they may at the same time bear plurilocular sporangia. There

[1] The opposite is reported for *Ectocarpus tomentosus* ((217) p. 360, (237) p. 126).

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can be no doubt that in defining these categories in this way the true state of affairs has been confused (299).

All filamentous stages derived from swarmers of unilocular sporangia must, until evidence to the contrary is forthcoming, be regarded as haploid; they are potential gametophytes and the reproductive organs they bear are gametangia. The frequent apogamous development of their swarmers may or may not be a natural condition (cf. p. 126). It is important to note that, wherever the fate of the swarmers from unilocular sporangia has been studied among the more advanced Ectocarpales, the resulting prothalli bear *plurilocular sporangia only* (cf. (56) p. 11, (152) p. 32, (239) pp. 348, 353, (240) p. 145); there is, moreover, no good evidence that they ever give rise directly to the adult thallus.

The swarmers from the plurilocular sporangia of the prothalli have often failed in cultures to afford any evidence of sexuality, but have germinated direct to give similar prothalli bearing similar sporangia, and in certain instances several successive generations of such stages have been obtained. These are some of the plethysmothalli of Sauvageau. They are, however, certainly different in nature from the plethysmothalli formed from the swarmers of the plurilocular sporangia of the sporophyte (cf. below). This is in agreement with the opinions expressed by Kylin ((152) pp. 32, 36, 66).

It is possible that extensive apogamous development of the gametes may take place in nature as in cultures, and that a succession of gametophytes is formed, of which the ultimate one produces gametes capable of sexual fusion and thus re-establishes the diploid phase ((128) p. 20); alternatively, the first-formed gametophyte may give rise to zygotes which develop a succession of similar plethysmothalli. Perhaps this is one means of perpetuation during the unfavourable period of the year. The fact, however, that sexual fusion has so rarely been observed in cultures may not be taken as a definite indication of its scarcity or absence in nature, since the conditions afforded by laboratory cultures are only too likely to be somewhat abnormal. In this connection attention may be drawn to the fact that in *Asperococcus bullosus* Sauvageau ((239) p. 386) failed to observe sexual fusion,[1] whereas this has now been established (129); the same is true of *Mesogloea vermiculata* (cf. (72) p. 7 and (152) p. 50 with (187) p. 36), *Spermatochnus paradoxus* (cf. (240) p. 128 with (186)), and *Castagnea virescens* (cf. (152) p. 57 and (239) p. 284 with (187) p. 37).

The diploid swarmers from the plurilocular sporangia of the macroscopic plant give rise to filamentous stages quite similar to the gametophytes (figs. 26 D, E; 47 M), but in no instance among the many studied has a sexual fusion of the swarmers they produce been

[1] Kylin's ((151) p. 18) record of fusion of the swarmers from the plurilocular sporangia of the ordinary individuals of this species is later described as erroneous ((152) p. 38).

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observed. It is for these minute diploid stages that, in my opinion, the term *plethysmothallus* should be reserved ((74) p. 130, (152) p. 86, (299)). Mostly they bear plurilocular sporangia, from which a succession of such (presumably diploid) plantlets can be produced (cf. e.g. (230), (239) p. 280, (240) p. 139); sometimes, however, they form both kinds of sporangia, as in *Myriotrichia repens* and *M. adriatica* ((240) pp. 64, 68) and *Litosiphon pusillus* ((152) p. 29, (244) p. 7; fig. 47 M), although this appears to be unusual.[1]

A feature, which speaks strongly in favour of the diploid nature of the plethysmothalli, is that sooner or later they commonly give rise directly (figs. 31 H, *e*; 47 M, *e*) to new plants (probable sporophytes; cf. (152) pp. 36, 65, (239) pp. 344, 360, 407). In other words their erect threads are capable of developing into the macroscopic plant as soon as conditions render this possible. In cultures of the diploid swarmers from the plurilocular sporangia of the sporophyte,[2] therefore, a succession of plethysmothalli may be obtained or a new sporophyte may be produced at an early stage. Which of the two occurs, no doubt depends not only on the season of the year in which the cultures are set up, but also, and perhaps more generally, on conditions in the cultures being suitable for the development of the macroscopic plant.

The plethysmothallus may give rise to the sporophyte as a lateral outgrowth, without itself producing any reproductive organs and, when this is so, Sauvageau speaks of a *protonema*. In such instances, however, as always among Ectocarpales, the adult thallus is merely an erect branch or branches of the primary heterotrichous stage constituting the so-called protonema. Its mode of development does not differ from that found in those plethysmothalli which simultaneously bear plurilocular (sometimes also unilocular) sporangia (fig. 47 M). Such differences appear to be fortuitous, the plethysmothallus being sterile or fertile according to circumstances, and I am of the opinion that no importance is to be attached to such variations. The diploid plethysmothallus must be regarded as a sporophyte (299), which remains for long periods arrested at the ectocarpoid stage, during which it can multiply by swarmers from plurilocular sporangia; similarly, it may continue to form such swarmers on the primary filaments when some of its erect branches are developing into the macroscopic sporophyte (fig. 37 C). The succession of plants formed from the diploid swarmers of the plurilocular sporangia of an *Ectocarpus siliculosus* or other simple form are just as much plethysmo-

[1] Diverse more complex relations are on record (cf. e.g. (241), (246) p. 132 regarding *Protasperococcus*), the evaluation of which is difficult, since it remains doubtful whether they represent a natural state of affairs.

[2] Possibly also of zygotes. For *Phloeospora brachiata* Mathias ((167) p. 16) makes it probable that the zygotes give rise within the host to endophytic filaments which do not grow to the surface until April.

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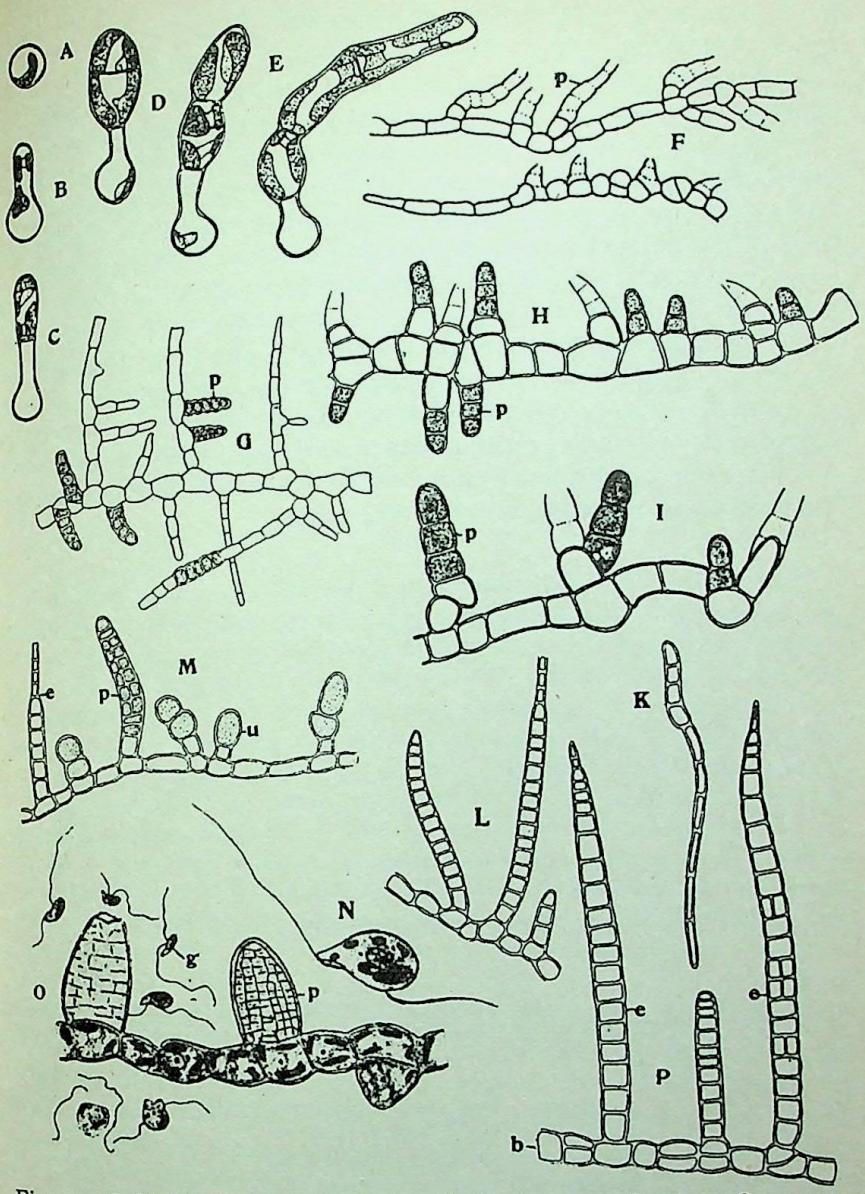

Fig. 47. A–E, H, *Stilophora rhizodes* J. G. Ag., germination of zoospores from unilocular sporangium; A, embryospore; B, first stage in germination; C, formation of first septum; D, E, later stages; H, mature gametophyte. F, *Dictyosiphon foeniculaceus* (Huds.) Grev., gametophyte. G, K–M, *Litosiphon pusillus* Harv.; G, gametophyte (from swarmers of unilocular sporangium); K, L, different stages of germination of swarmers from plurilocular sporangium; M, plethysmothallus. I, *Spermatochnus paradoxus* Kütz., mature gametophyte. N, O, *Phloeospora brachiata* Born.; N, zoospore; O, gametophyte. P, *Scytosiphon Lomentaria* (Lyngb.) Ag., development of young plants from swarmers of plurilocular sporangium. *b*, basal system; *e*, erect system; *g*, gamete; *p*, plurilocular sporangium and gametangium; *u*, unilocular sporangium. (F after Sauvageau; I after Papenfuss; N, O after Mathias; the rest after Kylin.)

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thalli; but here, owing to the non-elaboration of the sporophyte, the are in general identical in their morphological features with the latter

A large proportion of the advanced Ectocarpales thus evidently possess a life-cycle with a heteromorphic alternation. The diploid phase is constituted by the elaborate thallus, which bears either unilocular sporangia only or plurilocular ones as well, the latter there being most commonly produced at an earlier stage than the former. The haploid phase is a small filamentous plant bearing gametangia only. Either phase can probably propagate for several generations by means of small ectocarpoid stages, the diploid one by the swarmers from the plurilocular sporangia which give rise to plethysmothalli, the haploid one by means of apogamously developing gametes which give rise to accessory gametophytes. The plethysmothalli are to be regarded as arrested (juvenile) stages of the sporophyte. In how far this life-cycle can be short-circuited by the fusion of swarmers from the unilocular sporangia remains to be seen.[1]

Where both plethysmothalli and gametophytes are known, they do not in general appear to differ much in their vegetative structure, and sometimes there is almost complete identity ((239) p. 403). This is what one would expect on the view above propounded that the alternation is derived from an isomorphic one in which the one generation (the sporophyte) has been elaborated, while the other has remained at the stage of the simple filament. Certain differences in the early stages of germination and in the later growth are noted by Kylin ((152) p. 27) in *Litosiphon pusillus* (cf. also (234)), as well as by Sauvageau in *Punctaria latifolia* ((239) p. 342) and *Spermatochnus* ((246) p. 128), but in all such instances the differences are not fundamental. Sauvageau (227) records the persistence of sterile gametophytes over long periods.

[1] Appended is a list of the species of Ectocarpales in which heteromorphic alternation is probable on the basis of previous considerations (see also the list given on p. 130):

Castagnea Zosterae (?) ((152) p. 57, (233)).
Chordaria flagelliformis (239).
Desmotrichum undulatum (?) (152).
Hapterophycus canaliculatus (301).
Leathesia difformis ((56) p. 11, (152)).
Litosiphon pusillus (239).
Mesogloea Leveillei (?) (239).
Myrionema strangulans (?) (153).
Myriotrichia repens (240).
Nemacystus flexuosus (240).
Protasperococcus myriotrichiformis (240).
Punctaria latifolia ((239); cf. also (286)).
Stilophora adriatica (240).

Probably also in other Dictyosiphonaceae, apart from *Dictyosiphon foeniculaceus*.

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(c) Modified Types of Life-cycle

It is evident that some Ectocarpales show more or less marked departures from the type of life-cycle indicated above. In *Striaria attenuata* (153) and *Dictyosiphon Chordaria* ((72) p. 7), in which only unilocular sporangia have so far been found, the swarmers in cultures give rise to filamentous growths, which, after some time, produce erect branches that divide to form the adult thallus (fig. 35 B). Kylin ((153) p. 17; cf. also (129) p. 87) regards these forms as diploid ones in which reduction in the unilocular sporangium has been suppressed and on the available evidence this would appear to be the only valid interpretation. In *Hapterophycus* Hollenberg ((301), p. 682) found evidence of failure of meiosis in certain of the unilocular sporangia, and this possibly indicates how the condition in the species under consideration has arisen. It is to be noted that some of their immediate allies show a normal alternation.

In *Dictyosiphon Chordaria* Föyn succeeded in growing four successive generations without seeing any plurilocular sporangia. A similar condition seems to exist in *Asperococcus compressus* (194, 235), where, however, rare plurilocular sporangia have also been recorded ((239) p. 363). Sauvageau has grown new plants from the swarmers of the unilocular sporangia.

Other instances are afforded by *Pylaiella rupincola* (see p. 129) and *Elachista fucicola* ((154) p. 12). In *E. stellaris*, where the macroscopic plant also bears plurilocular sporangia, the swarmers from the unilocular ones can reproduce the plant directly. For all three Kylin advances the same explanation as above.

It has long been known that the thalli of *Scytosiphon*, *Petalonia*, and *Colpomenia* bear plurilocular sporangia only ((239) p. 402). Fusion of the swarmers (fig. 44 I) has repeatedly been reported in *Scytosiphon Lomentaria* ((1) p. 333, (27) p. 407, (75), (138), (145) p. 160); Kuckuck (145) also recorded such fusion in material of *Petalonia zosterifolia* from the Adriatic. Others ((56) p. 12, (152) p. 47, (239) p. 332) find that the swarmers of *Scytosiphon* give rise, without fusion, to a system of creeping filaments which may perhaps reproduce by plurilocular sporangia ((239) p. 333), but more usually (fig. 34 B, C) unite to form a disc and regenerate a new plant. For *Petalonia debilis* ((239) p. 323) and *P. Fascia* ((152) p. 44) it has likewise been shown that the swarmers can give rise to new plants direct (fig. 34 F). According to Sauvageau (232) a similar development occurs in *Colpomenia* (cf. p. 111), while Kunieda and Suto (148) record sexual fusion (cf. p. 124).

It is difficult to reconcile the data on direct development of a new thallus with the records of sexual fusion between the swarmers from the plurilocular sporangia. They suggest that there may be several types of the latter, and this is supported by the recent observations on *Colpomenia* (148). Kylin ((152) p. 46), who regards the three genera

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under discussion as diploid forms which have lost the unilocular sporangia, considers the fusions that have been described as misinterpretations. In this connection attention may be drawn to Reinke's ((194) p. 301) record of the occurrence of double zoospores in *Petalonia*, although he found no evidence of copulation. The possibility, however, that reduction might take place during the development of certain of the plurilocular sporangia cannot be altogether ruled out (cf. also (125) p. 156).

Much the same position exists in *Giraudya* (p. 124), where Sauvageau ((231) p. 46) records a succession of plethysmothalli before the adult thalli reappear. Several species of *Stictyosiphon* too are only known to possess plurilocular sporangia, although unilocular ones are found in *S. adriaticus* ((240) p. 160). Kuckuck ((145) p. 164) records fusion of the swarmers in *S. tortilis*, whereas Sauvageau ((239) p. 306) observed a direct development into new plants in *S. Corbierei*.

Mention must also be made of *Ascocyclus orbicularis*, in which direct development of new individuals from the product of germination of the swarmers of the plurilocular sporangia appears to be the rule (152, 229), although Sauvageau believes he has on one occasion obtained some evidence of sexual fusion. The recent discovery of unilocular sporangia (p. 60) supports the view that *Ascocyclus* is diploid and renders improbable the opinion expressed by Parke ((187) p. 38) that this alga is a stage in the life-cycle of *Castagnea Zosterae*.

STATUS AND CLASSIFICATION OF ECTOCARPALES

As mentioned at the outset the delimitation of Ectocarpales here adopted agrees essentially with that of Oltmanns.[1] The order, as thus circumscribed, is characterised primarily by its heterotrichy and the lack of true oogamy, as well as by the comparatively simple organisation of the thallus. There can of course be no serious objection to the elevation of some of the families or groups of families here recognised to ordinal rank, but the differences between them, save in vegetative construction, are slight and scarcely of the nature usually accepted for distinguishing major systematic units. With the discovery of heteromorphic alternation in *Dictyosiphon*, a new taxonomic feature became available and the separation of the Dictyosiphonaceae from other Ectocarpales was advocated (275). Sauvageau ((230*a*) p. 191), with more reason, later established the order Sporochnales (p. 171).

Recently Kylin ((152) p. 91; cf. also (278)) has laid special stress on the features of the life-cycle in the classification of the Phaeophyceae as a whole, distinguishing a series Isogeneratae, with isomorphic, from another series Heterogeneratae, with heteromorphic alternation; to the former he refers Ectocarpales (sens. limit.), Sphacelariales, Cutleriales, Tilopteridales, and Dictyotales, to the latter Chordariales, Sporochnales, Desmarestiales, Punctariales, Dictyosiphonales, and

[1] For a brief account of earlier systems of classification, see (152) p. 89.

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Laminariales. The Ectocarpales are restricted to those forms that show isomorphic alternation (Ectocarpaceae, some Myrionemataceae)[1] and, since they include both simple filamentous types and crust-forming genera, exhibit a considerable vegetative range. Chordariales, Punctariales, and Dictyosiphonales are distinguished only on vegetative grounds.

In the preceding section the view has been advanced that forms with heteromorphic alternation are to be regarded as derived from filamentous isomorphic types by divergent development of the two phases. If this view be accepted, a classification based on the life-cycle is scarcely feasible among the simpler Brown Algae. Moreover the Punctariaceae and their allies, for example, are closely linked by way of such forms as *Phloeospora* with the simple filamentous types, and it scarcely appears advisable to class them in a separate order. All the diverse kinds of thallus-development among Ectocarpales are, in fact, derivable from simple filamentous types, such as are illustrated by the Ectocarpaceae. On the other hand, both Sporochnales and Desmarestiales not only show a very marked degree of vegetative specialisation in different directions, but exhibit true oogamy which, so far as present evidence goes, is never realised in the Ectocarpales. Both the former are indeed as sharply characterised as the Cutleriales, which have long been classed as a distinct order.

It is scarcely feasible to trace in further detail the lines of evolution that have resulted in the diverse types of structure met with among Ectocarpales. Their interrelation depends largely on their derivation from a common filamentous type. Two significant evolutionary advances were the inception of longitudinal septation, leading to the parenchymatous (polystichous) habit, and the substitution of apical for trichothallic growth which is seen in both the big series of Ectocarpales (Spermatochnaceae, Dictyosiphonaceae). It is also noteworthy that, among the polystichous forms, there is commonly a tendency for the aggregation of the sporangia into sori, accompanied by the development of associated paraphyses which probably often fulfil a protective function.

In adding an epitome of the classification here adopted, it may be emphasised that it is essentially one of convenience and that a larger number of families should no doubt be distinguished; the exact relationships of a considerable number of the genera are, moreover, at present scarcely clear.

(*a*) Simple and in part probably primitive forms:

1. *Ectocarpaceae:* Ascocyclus, Bodanella, Ectocarpus, Geminocarpus, Mikrosyphar, Phaeostroma, Pleurocladia, Pylaiella, Sorocarpus, Streblonema, Streblonemopsis, Zosterocarpus (?).

[1] It is suggested that some of these may be reduced Mesogloeaceae. All certainly do not appear to be isomorphic. Even in certain species of *Ectocarpus* there are some indications of heteromorphy (p. 128).

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(*b*) Haplostichous forms:

2. *Myrionemataceae:* Chilionema, Compsonema, Hecatonema, Heribaudiella, Lithoderma, Mesospora, Microspongium, Myrionema, Nemoderma, Petroderma (?), Ralfsia, Symphyocarpus.

3. *Elachistaceae:* Elachista, Giraudya (?), Halothrix, Leptonema, Symphoricoccus.

4. *Leathesiaceae:* Corynophlaea, Cylindrocarpus, Leathesia, Myriactula.

5. *Mesogloeaceae:* Analipus (?), Bactrophora, Caepidium (?), Castagnea (incl. Eudesme), Chordaria, Gontrania, Haplogloea, Haptophycus (?), Heterochordaria (?), Mesogloea, Myelophycus (?), Myriocladia, Myriogloea, Sphaerotrichia, Strepsithalia.

6. *Acrotrichaceae:* Acrothrix.

7. *Spermatochnaceae:* Chordariopsis, Halorhiza, Nemacystus, Spermatochnus, Stilophora, Stilopsis.

8. *Splachnidiaceae:* Splachnidium.

(*c*) Polystichous forms:

9. *Punctariaceae:* Corycus, Desmotrichum, Litosiphon, Omphalophyllum, Phaeosaccion, Phloeospora, Punctaria, Stictyosiphon, Xanthosiphonia.

10. *Asperococcaceae:* Asperococcus, Isthmoplöea, Myriotrichia, Petalonia (Phyllitis, Ilea), Protasperococcus, Scytosiphon, Striaria.

11. *Encoeliaceae:* Chnoospora, Cladochroa, Colpomenia, Hydroclathrus, Iyengaria, Soranthera.

12. *Dictyosiphonaceae:* Coilodesme, Delamarea, Dictyosiphon, Scytothamnus.

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Order II. *TILOPTERIDALES*

The few filamentous Algae included in this order are usually found in the sublittoral region, often at some depth, and so far have been recorded almost only from the Atlantic shores of Europe and North America ((28) p. 136).[1] Although widely distributed, they are sporadic in their occurrence and are mostly found only for a brief period during spring ((23) p. 59). As a consequence our knowledge of Tilopteridales, and especially of the life-cycle, is imperfect. Certain peculiar features, in particular the large motionless monospores formed singly within a sporangium (fig. 50 B), have been given diverse interpretations.

The order was created in 1855 by Thuret (29) who, recognising that the *Ectocarpus Mertensii* of Harvey ((7) pl. 132) possessed motionless monospores, assigned it to a new genus *Tilopteris*. Subsequently Kjellman ((10) p. 3) added a second genus *Haplospora*, later studied more fully by Reinke (19). To this genus Bornet ((3) p. 363) referred *Ectocarpus Vidovichii* Kütz. (*E. geminatus* Menegh.), although Kuckuck (13) subsequently placed this species in a distinct genus *Heterospora*. Bornet ((3) p. 370) also established for *Ectocarpus pusillus* Griff. ((7) pl. 153, (20)) (*E. ostendensis* Askenasy (1) p. 785) a genus *Acinetospora*, distinguished by the production of large scarcely mobile spores from

[1] The *Scaphospora* (?) *Kingii* of Farlow ((6) p. 67) is probably a form of *Haplospora globosa*.

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the plurilocular sporangia. Later Sauvageau (22) showed that *A. pusilla* possessed monospores, as well as unilocular sporangia, and referred it to the Tilopteridales. He also concluded that there were no grounds for the generic separation of *Heterospora* and *Acinetospora*. Since the latter name has priority, *Heterospora Vidovichii* becomes *A. Vidovichii*, and this has been followed here. Sauvageau ((22) p. 117) draws attention to the close resemblance between *Ectocarpus crinitus* Carm. ((3) p. 361) and *Acinetospora pusilla*. Newton ((16*a*) p. 211) lists it as a variety of the latter species.

VEGETATIVE FEATURES

As the preceding paragraph shows, nearly all Tilopteridales have in the past been placed in the genus *Ectocarpus*, which is due to the similar habit and arrangement of the reproductive organs. The well-branched plants, which possess a heterotrichous habit, form tufts attached to diverse substrata, those of *Tilopteris* often occurring on mud-covered rocks. The prostrate system is incompletely known, but Sauvageau ((23) p. 74) describes a compact basal disc in *Tilopteris* (fig. 48 A) and Reinke's data ((19) p. 108) for *Haplospora* indicate a similar condition. The erect filaments of *Acinetospora* (incl. *Heterospora*) are uniseriate throughout (figs. 48 F, G; 49 A), but in *Tilopteris* and *Haplospora* (fig. 48 J) the lower parts become multiseriate and in their regular septation recall a *Sphacelaria*. Growth in the Tilopteridales is, however, always intercalary (fig. 48 F), the diverse branches usually terminating in hairs (*h*) with a basal meristem (*me*). In addition to this well-marked trichothallic growth, the longer threads usually show other regions of active division (fig. 48 G, *me*; (9) p. 106), as in some species of *Ectocarpus* (p. 54).

The branches generally arise from the top of the parent cell, but in *Acinetospora* both they and the reproductive organs commonly grow out from its middle (fig. 49 D). In *A. pusilla* the numerous short and spine-like branches serve to link the filaments with one another, as well as with those of other algae ((2) p. 30, (3) p. 357). Rhizoids, which sometimes show longitudinal division, often arise in some numbers from the lower cells. The cells contain a considerable number of chromatophores; pyrenoids are only recorded in *Acinetospora Vidovichii* ((13) p. 295, (26) p. 165).

THE REPRODUCTIVE ORGANS

Characteristic of the order are the globose or oblong *monosporangia*, which are generally situated at the ends of short, often one-celled, laterals (figs. 48 L; 49 A, *m*), although commonly sessile in *Acinetospora pusilla* ((22) p. 110). In *Tilopteris*, where they are usually paired, they occupy an intercalary position (fig. 48 B, *m*). As a general rule the entire contents are liberated as a single monospore (fig. 50 A, B), which is usually provided with a firm but delicate membrane. The

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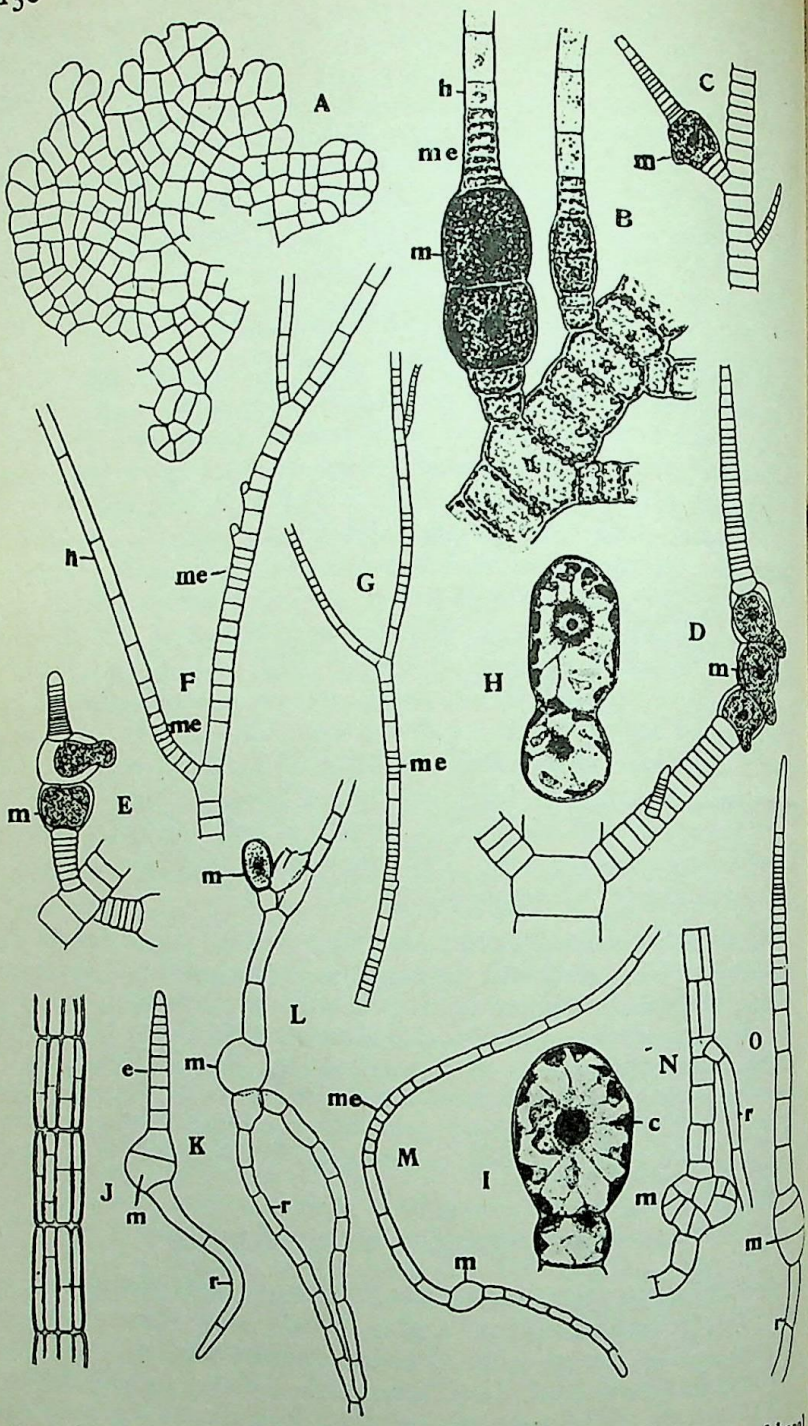

Fig. 48. A–E, K, N, O, *Tilopteris Mertensii* (Ag.) Thur.; A, part of basal stratum; B, part of an erect thread with intercalary monosporangia (*m*); C, D, germination of monospores *in situ*; E, liberation of monospores;

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relatively wide aperture of the sporangium is in *Tilopteris* lateral in position (fig. 48 E). The cytoplasm of the spore is markedly alveolar (fig. 50 A, B). Division of the nucleus into four or more (up to twelve) parts (fig. 50 A) has in certain instances been reported before the liberation of the spore. Germination has frequently been observed ((29) p. 7) and not uncommonly occurs within the sporangium (fig. 48 C, D).

In *Tilopteris* ((23) p. 81) formation of a rhizoid (fig. 48 K, *r*) is followed by the outgrowth of a thread (*e*) from the opposite end; subsequently the body of the spore may become divided by septa in diverse directions (fig. 48 N, *m*). A similar type of germination is recorded ((19) p. 116) in *Haplospora*, although in cultures division of the quadrinucleate spore into four parts, prior to the outgrowth of either rhizoids or threads, was observed; Reinke regarded this as the normal method of germination, but this is not supported by Sauvageau's observations. In *Acinetospora pusilla* ((22) p. 113), *A. Vidovichii* ((13) p. 298), and *Tilopteris* ((5) p. 14) a new generation producing monospores has been grown from the monospore.

Plurilocular sporangia are known in all genera and are always accompanied by monosporangia. In *Tilopteris* ((3), (29) p. 6) and *Haplospora* ((19) p. 130) they are usually situated at or near the bases of the branches (fig. 49 E, H, *pl*), although in *Haplospora* they sometimes constitute the entire lateral. The numerous small compartments of these sporangia (fig. 49 E, *pl*) contain only one or two chromatophores and form a single series surrounding a central hollow (*i*); the individual compartments open separately to the exterior. The swarmers in *Tilopteris* (fig. 49 G) ((14) p. 182, (29) p. 7) are hyaline with a red eye-spot (*s*) and are stated to resemble the spermatozoids of *Fucus*; Reinke's incomplete data for *Haplospora* ((19) p. 133) indicate similar features. The plurilocular sporangia of these two genera in fact show most, if not all, the characteristics of antheridia and, since Thuret's time, have generally been interpreted in this sense.

The plurilocular sporangia of *Acinetospora*, on the other hand, are of a different nature ((3) p. 356, (26) p. 166).[1] They are always terminal on short laterals, possess relatively few and large compartments, and are without a pronounced central hollow (fig. 49 D). The swarmers

[1] Those described by Hauck ((8) p. 221) for *Ectocarpus geminatus* (*Acinetospora Vidovichii*) do not belong to this species.

K, N, O, germlings from monospores. F–I, M, *Acinetospora Vidovichii* (Kütz.) Sauv.; F, G, parts of vegetative threads; H, I, monosporangia; M, germinating monospore. J, *Haplospora globosa* Kjellm., polysiphonous basal part of a thread. L, *Acinetospora pusilla* (Griff.) Born., germling of monospore, with monosporangium. *c*, chromatophore; *e*, erect thread; *h*, hair; *m*, monosporangium or monospore; *me*, meristem; *r*, rhizoid. (B after Bornet; F, G, M after Kuckuck; H, I after Schussnig; J after Reinke; the rest after Sauvageau.)

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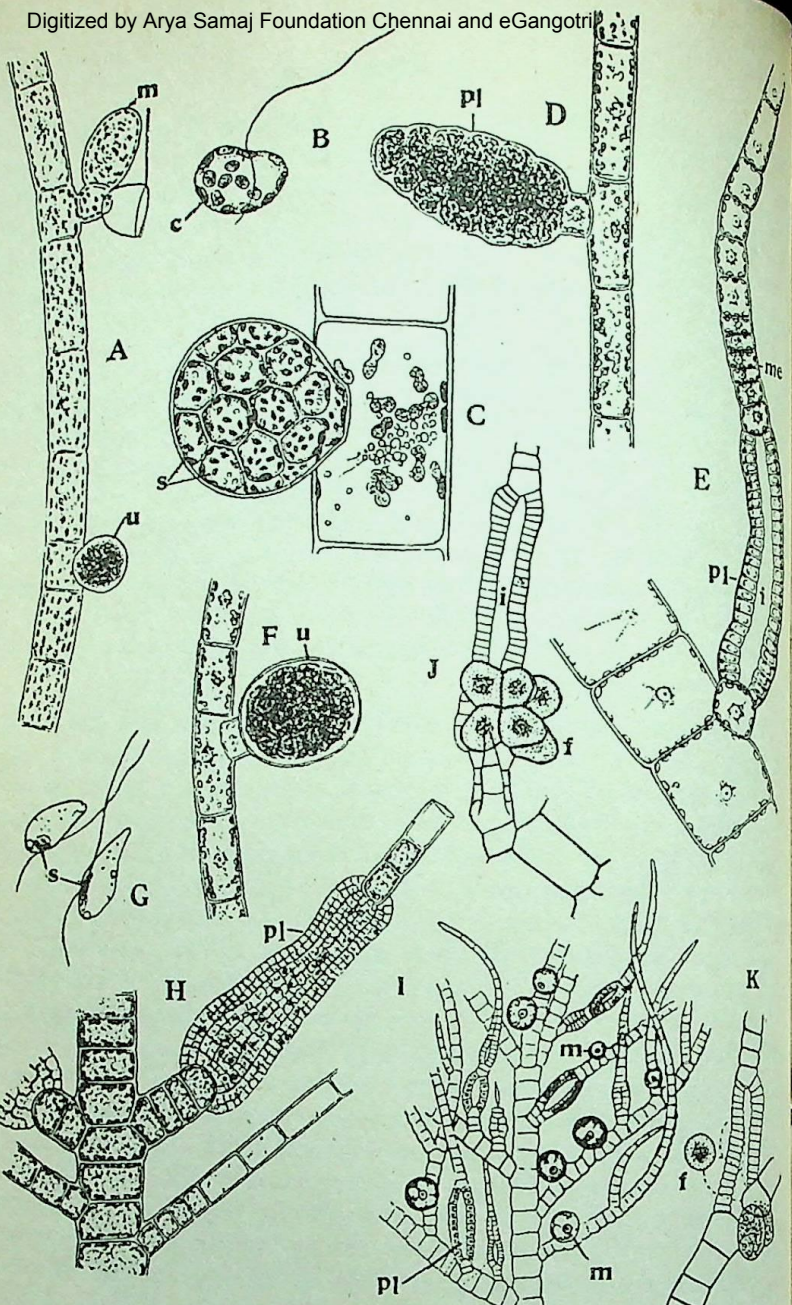

Fig. 49. A–C, *Acinetospora Vidovichii* (Kütz.) Sauv.; A, thread with monosporangia and unilocular sporangium; B, zoospore; C, almost mature unilocular sporangium. D, F, *A. pusilla* (Griff.) Born., pluri- and unilocular sporangia respectively. E, I, *Haplospora globosa* Kjellm. (*Scaphospora speciosa* Kjellm.); E, plurilocular sporangium (antheridium?); I, part of a plant with plurilocular sporangia and monosporangia. G, H, J, K, *Tilopteris Mertensii* (Ag.) Thur.; G, spermatozoids; H, part of thread with plurilocular sporangium; J, K, plurilocular sporangia with larger basal compartments. *c*, chromatophore; *f*, possible female gamete; *i*, central cavity of plurilocular sporangium; *m*, monosporangium; *me*, meristem; *pl*, plurilocular sporangium; *s*, stigma; *u*, unilocular sporangium. (D, F, H after Bornet; E after Reinke; I after Brebner; J, K after Dammann; the rest after Kuckuck.)

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(fig. 49 B), which commonly behave as aplanospores, are large and provided with several chromatophores ((21) p. 33). They germinate readily ((22) p. 109) and grow into plants again bearing plurilocular sporangia (25). Recently Dammann ((5) p. 15; cf. also (3) p. 368) records at the base of the "antheridia" of *Tilopteris* (fig. 49 J, *f*) large, dark brown compartments, with abundant chromatophores, the contents of which are liberated (fig. 49 K) as amoeboid spores; some of these grow out into short filaments, although the majority fail to germinate. It is possible that these large compartments are to be compared with those of the plurilocular sporangia of *Acinetospora*, although they occur in the same organ as produces the supposed spermatozoids.

Unilocular sporangia, producing a number of large swarmers similar to those of the plurilocular sporangia ((22) p. 109), are recorded only in *Acinetospora* (fig. 49 C, F); the swarmers are devoid of an eye-spot. In *A. pusilla* they are found on the same plants as bear the plurilocular sporangia, whilst in *A. Vidovichii* ((13) p. 299) they apparently occur on distinct individuals; in the former species the zoospores have been observed to germinate within the sporangium.

Vegetative reproduction takes place readily from fragments of the threads, which easily form rhizoids ((19) p. 109, (22) p. 116, (23) p. 77). Sauvageau ((23) p. 84; cf. also (5) p. 15) also records the formation of akinetes from the prostrate system and the lower polysiphonous portions of the erect threads in *Tilopteris* (fig. 50 C, D, *a*) and suggests that these structures constitute a means of perennation.

THE PROBLEMS PRESENTED BY THE LIFE-CYCLE

In *Haplospora* there are two kinds of individuals (19), the one producing monosporangia only, the other (fig. 49 I) with monosporangia and the above described "antheridia". The second was first recorded ((11) p. 29) as a separate genus *Scaphospora*[1] (cf. also (4) p. 179), but since Reinke's memoir *Scaphospora speciosa* Kjellm. (incl. *S. arctica*) has generally been regarded as a phase of *Haplospora globosa*. There appear to be no vegetative differences between the two plants. Reinke established that the *Haplospora*-individuals liberate a quadrinucleate monospore provided with a definite membrane (fig. 50 A), whereas the monosporangia of the *Scaphospora*-plants set free a naked uninucleate spore (fig. 50 B, *m*). In *Haplospora* the monosporangia are generally borne terminally on short lateral branches (fig. 50 A), whilst in *Scaphospora* ((19) p. 127) they are partly immersed in the threads and generally arise after a longitudinal division from half the parent-cell (figs. 49 I, *m*; 50 B); both halves may, however, develop into monosporangia or the latter may be produced without division. Exceptionally the sporangia occupy a similar position on the *Haplospora*-individuals ((19) p. 112).

[1] *Capsicarpella speciosa* ((10) p. 26).

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These facts led Reinke to conclude that there was an isomorphic alternation between an asexual *Haplospora*-phase producing quadrinucleate monospores, homologous with the tetraspores of Dictyotales, and a sexual *Scaphospora*-phase bearing oogonia and antheridia, the monosporangia liberating naked uninucleate spores on these individuals being interpreted as female organs.[1] Nienburg ((17); cf. also (5) p. 21) described synezesis and an indistinct diakinesis stage during monospore-formation in *Haplospora globosa*, thus affording some

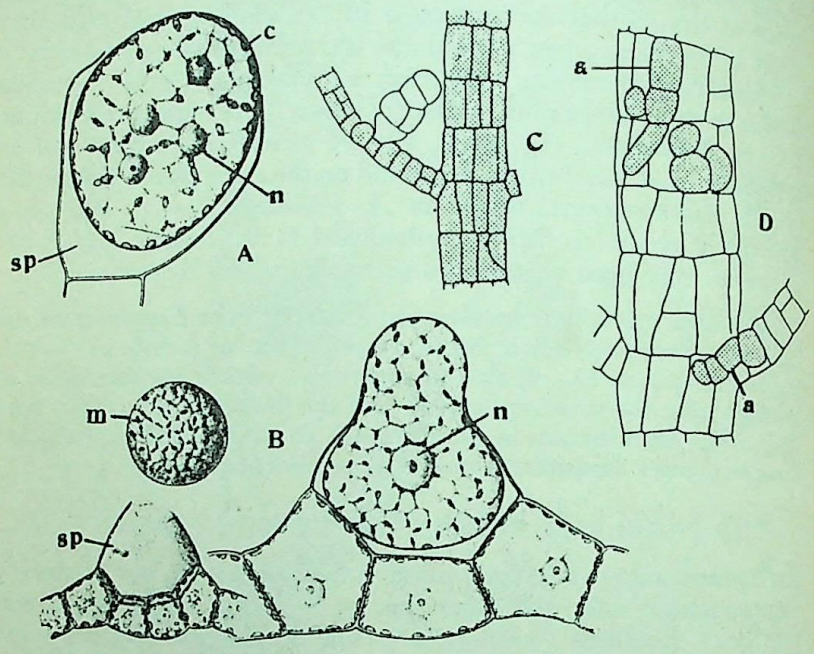

Fig. 50. A, B, *Haplospora globosa* Kjellm.; A, liberation of quadrinucleate monospore; B, liberation of uninucleate monospores on the *Scaphospora*-individual. C, D, *Tilopteris Mertensii* (Ag.) Thur., formation of akinetes. *a*, akinete; *c*, chromatophore; *m*, monospore; *n*, nucleus; *sp*, sporangium. (A, B after Reinke; C, D after Sauvageau.)

evidence for the occurrence of a reduction division, although the data for halving of the chromosome-number are scarcely satisfactory. All those who have studied this genus (4, 11, 19) report a great scarcity of *Scaphospora*-individuals; on the shores of Heligoland, where *Haplospora* is frequent, *Scaphospora* has never been found (17).

In *Tilopteris Mertensii* Reinke ((19) p. 156) observed two, four, or sometimes more, nuclei in monospores provided with a membrane and derived from plants bearing these structures only. He therefore

[1] Brebner's ((4) p. 178) record of the presence of "antheridia", and of uni- and quadrinucleate monospores on the same plant, has been regarded as an abnormality by various subsequent writers.

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concluded that the individuals in question represented the asexual phase of this species, while the plants previously recorded by Thuret, which formed both monosporangia and "antheridia", were regarded as constituting the sexual phase. Reinke thus assumed that *Tilopteris* showed the same isomorphic alternation as *Haplospora*, although in the former genus there is no difference either in position or form between the monosporangia of the asexual plant and the supposed oogonia of the sexual individual; no cytological data are available. Kuckuck ((14) p. 181) found but few individuals of *Tilopteris* with antheridia, while the monospores in his material were always naked and uninucleate.

Reinke's hypothesis as to the nature of the life-cycle has been accepted by various authorities ((12) p. 178, (15), (16) p. 92, (18) p. 175), although there is no evidence of fertilisation, nor of any attraction of the spermatozoids by the naked uninucleate monospore (14). There is thus at present nothing to show how the diploid state is re-established; yet, if the *Haplospora*- and *Tilopteris*-plants bearing monospores only are asexual and the observations as to the occurrence of reduction are correct, then there must be a nuclear fusion to restore the diploid state. A further objection lies in the absence of any parallel for the complete similarity between monosporangia and female organs as is postulated by Reinke's theory. Sauvageau also emphasises the great range in size of the uninucleate monospore, a feature which is very unusual in a sexual cell.

Acinetospora, in which "antheridia" are unknown and the monospores are always uninucleate and provided with a membrane before liberation ((13) p. 295, (22) p. 110), does not fit into the theory at all. Kylin ((15) p. 306), in fact, regards this genus as having no affinity with the others. It must be recognised, however, that *Acinetospora* shows considerable similarities, both in structure and other respects, with the other two genera; much emphasis cannot be laid on the absence of longitudinal division.

A somewhat different complexion has been put on the problem by the demonstration that *Tilopteris* liberates two kinds of reproductive cells from its plurilocular sporangia, viz. "spermatozoids" and others which resemble the units produced from the plurilocular sporangia recorded for the two species of *Acinetospora* (p. 151). The latter may represent female gametes[1] ((5) p. 18), and further investigation may disclose the presence of antheridia in *Acinetospora*. The Tilopteridales would then show anisogamy comparable to that of Cutleriales. On this view the monosporangia, of the sexual individuals at least, would be relegated to the position of accessory asexual reproductive organs,

[1] Schmidt's observation (25) that the swarmers may produce a succession of individuals with pluri- or unilocular sporangia, in view of the frequent apogamy recorded in cultures of Ectocarpales, does not speak against this hypothesis.

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an interpretation which Sauvageau has maintained since 1899 (22; 23). The fact that some individuals possess these structures only is paralleled by what is known of the distribution of reproductive organs in other series of the lower Brown Algae.

Sauvageau regards the monospores as organs of vegetative propagation comparable to the propagules of Sphacelariales, a view based largely on the structural resemblances between them and the propagules of *Choristocarpus* (p. 297). The monospores of Tilopteridales are, however, clearly spores and the organs which produce them sporangia. They are better interpreted as modified unilocular sporangia ((26) p. 169) which, so far as present evidence goes, have altogether replaced the usual type in *Tilopteris* and *Haplospora*. A cytological study can alone shed light on these matters and settle the rôle of the unilocular sporangia, which are known in *Acinetospora* only. In this genus they may prove to be the seat of the reduction divisions, whilst in the other two, on present evidence, these would appear to take place in the monosporangium of the asexual individuals. *Acinetospora* seems to be the most primitive member of the order.

In their trichothallic growth and simple filamentous habit the Tilopteridales appear as an offshoot of the Ectocarpales. They show specialisation, however, in diverse respects, viz. in the monospores, in the differentiated "antheridia", in the tendency towards a multiseriate construction, and in the specialised unilocular sporangia of *Acinetospora*. On the other hand the affinity with Sphacelariales, which some have supported, does not appear to be based on any strong evidence, and such resemblances as there are are likely to be due to parallel development. The correspondence between the propagules of *Choristocarpus* (p. 297) and the monosporangia of Tilopteridales is, however, certainly striking. The distinctive features are sufficiently marked to warrant regarding the Tilopteridales as an order allied to, but distinct from, the main body of the Ectocarpales.

The genus *Masonophycus*, established by Setchell and Gardner ((27) p. 141) and doubtfully referred to this order, is distinguished by the possession of tetrasporangia producing four cruciate spores. At present so little is known about it, that its reference to a separate family (24) appears premature.

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Order III. *CUTLERIALES*

Cutleria and *Zanardinia*, the only known members of this order, would hardly merit separation from Ectocarpales on the basis of their vegetative structure. The anisogamous sexual reproduction, however, falls little short of the oogamy of the more specialised Phaeophyceae, whilst the alternating generations of *Cutleria* imply an advance from isomorphic to heteromorphic alternation which is probably significant as an indication of specialisation. The life-cycle of *Cutleria* presents many complications, but these will be reserved for later discussion (p. 165) and the normal sequence will first be considered.

The species of *Cutleria* ((23), (25), (37) p. 21) are annuals, occurring in the sublittoral region for a few months during the favourable period of the year. *C. multifida* and *C. adspersa* ((40) p. 67), the latter mainly confined to the Mediterranean, the former known also in northern latitudes, are found in relatively shallow water ((20*a*) p. 74), whilst the Mediterranean *C. monoica* ((20), (20*a*) p. 115) occurs at depths of 20–80 metres. *C. multifida* (fig. 51 A) has a repeatedly branched band-shaped thallus, up to 20 cm. in length; all the branches usually lie in one plane and terminate in tufts of assimilatory hairs (*a*). *C. monoica* is similar but smaller, whilst *C. adspersa* (fig. 51 I) has a

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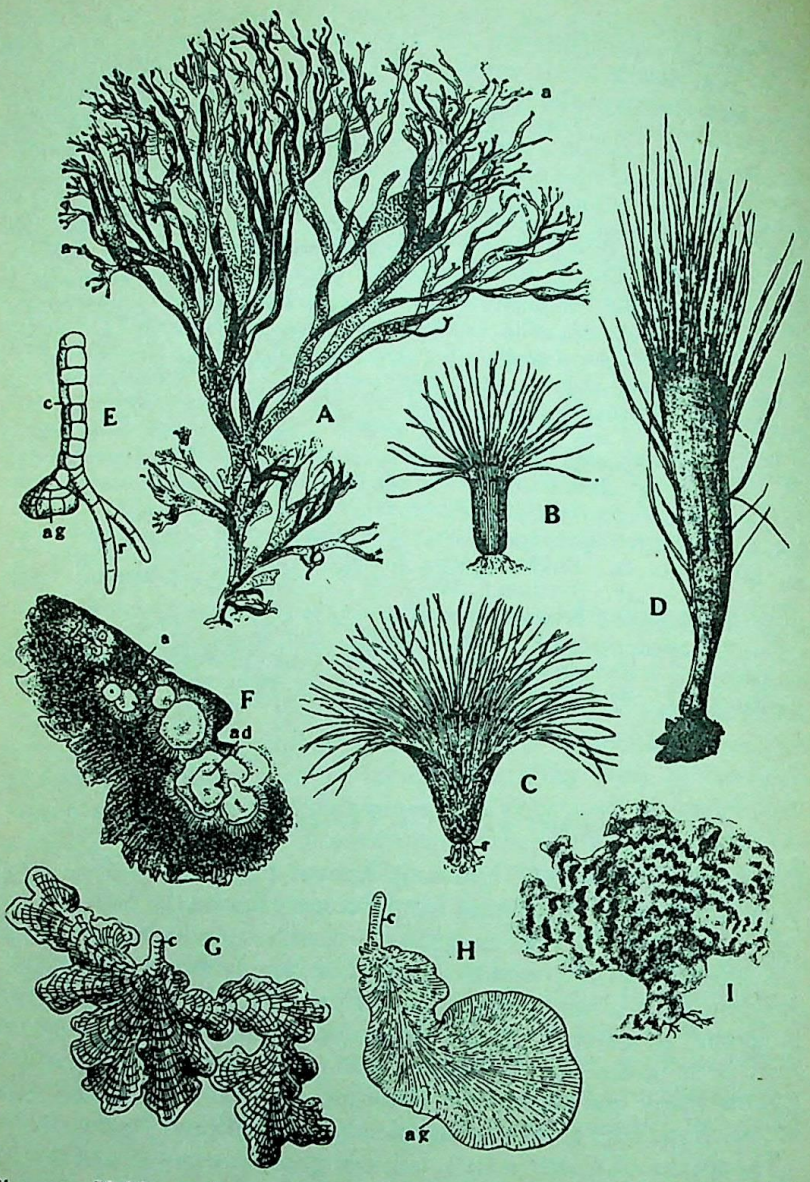

Fig. 51. Habits and young stages of Cutleriales. A, D, E, G, *Cutleria multifida* (Smith) Grev.; A, mature gametophyte; D, young plant; E, early stage of germination of zygote; G, sporophyte (*Aglaozonia*-stage). B, C, H, I, *C. adspersa* (Roth) De Not.; B, C, two successive stages in development of gametophyte; H, young sporophyte (*Aglaozonia*-stage); I, mature gametophyte. F, *Zanardinia collaris* (Ag.) Crouan, part of an old plant, showing a number of young ones (*ad*) developed adventitiously. *a*, free assimilatory filaments; *ag*, the *Aglaozonia*-crust; *c*, the column of the *Aglaozonia*-stage; *r*, rhizoid. (A after Thuret & Bornet; B, C, H after Sauvageau; D after Kuckuck; E, G after Falkenberg; F after Reinke; I after Janczewski, from Oltmanns.)

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lobed fan-shaped thallus bearing numerous assimilatory hairs along its margin.

These plants are gametophytes bearing gametangia of two kinds (fig. 53 A, G), usually on distinct individuals which may show certain inconstant differences ((38) p. 446). *C. monoica*, however, is monoecious, the two kinds of gametangia sometimes even occurring in the same sorus ((20), (32) p. 17; cf. (7) p. 167). The zygote develops into a flat encrusting thallus of considerable size, known as the *Aglaozonia*-stage (fig. 51 G). These crusts are apparently perennial and represent the resistant phase in the life-cycle; they grow permanently submerged like the gametophytes and can evidently flourish at appreciable depths (10). They were long regarded as species of a distinct genus, *Aglaozonia*. It is now known, however, that *A. parvula* (*A. reptans*) is the sporophyte of *C. multifida*, *A. melanoidea* (28) that of *C. adspersa*, and *A. chilosa* that of *C. monoica*. The *Aglaozonia*-stage produces on its upper surface dense sori of unilocular sporangia (fig. 54 A), the swarmers of which reproduce the gametophyte.

Zanardinia collaris Crouan[1] ((4), (22), (23) p. 69, (24) p. 320, (25) p. 286, (40) p. 71), which is probably perennial, is likewise a deep-water form known mainly from the Mediterranean, although it is reported from the Azores ((35) p. 29) and occurs as far north as the Channel Islands. The thallus (fig. 51 F), which takes the form of a rounded disc, leathery in texture and 4–20 cm. in diameter, somewhat resembles a shallow *Peziza*; older plants are often irregular in shape with parts of the margin worn away. The discs sometimes possess a slight stalk (cf. fig. 52 G) and their edge is fringed with assimilatory hairs (fig. 51 F, *a*). The plants are either sexual or asexual, the two generations being alike; the sexual phase is monoecious (fig. 53 B). In both genera reduction occurs at the first division in the unilocular sporangium (38, 39).

THE SEXUAL PHASE

Although so different in outward habit, the gametophytes of both genera show essentially the same trichothallic mode of growth and the same ultimate structure (23, 25). The peripheral assimilatory hairs, the cells of which contain abundant chromatophores, usually form two superposed series (fig. 52 A). At the base of each hair lies an intercalary meristem (fig. 52 A, B, *m*), giving off segments both to the outside and to the inside. Those cut off externally contribute to the lengthening of the hairs, whilst those formed below the meristem undergo further transverse and longitudinal septation (fig. 52 A, B, G) and, with some tangential enlargement, fuse to form the compact tissue (*t*) of the thallus a short distance beneath the individual

[1] This is probably the *Zonaria collaris* of Harvey ((10*a*) pl. 359). Feldmann (7) p. 165) considers that this species should be called *Z. prototypus* Nardo.

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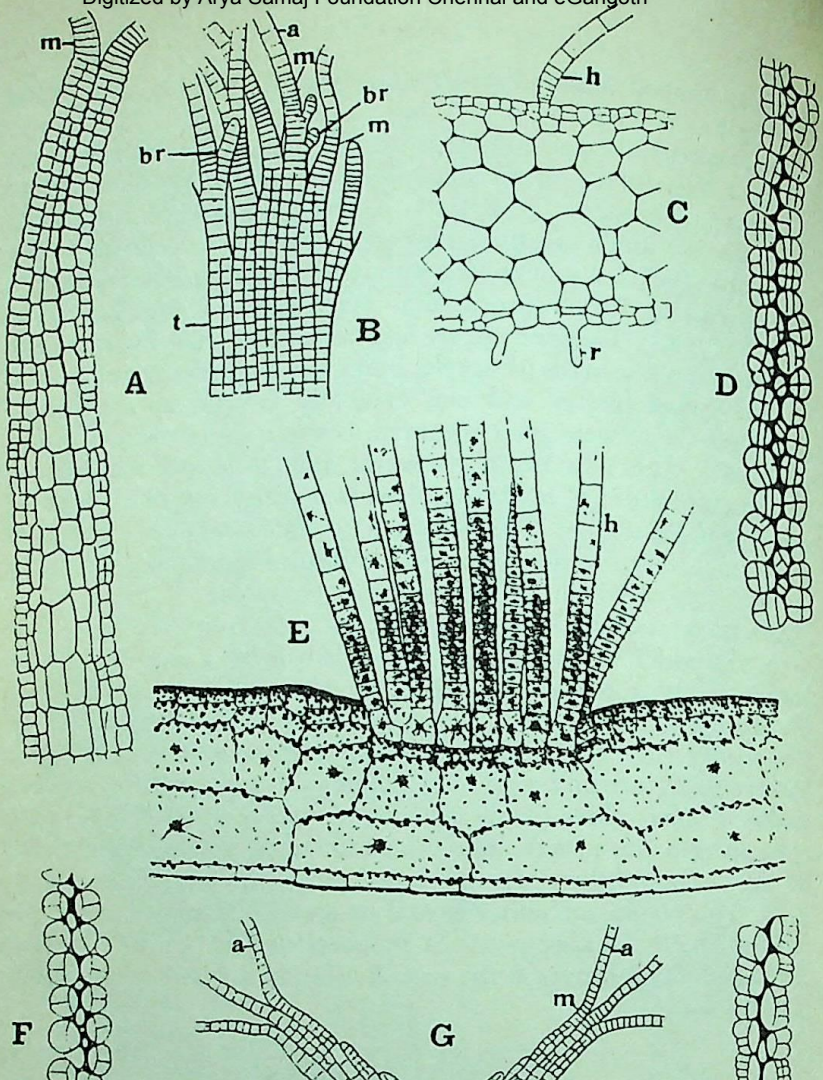

Fig. 52. Structure of thallus in Cutleriales. A–D, G, *Zanardinia collaris* (Ag.) Crouan; A, radial longitudinal section of growing margin; B, the same from above; C, part of transverse section of disc, some way from growing margin; D, transverse section near margin; G, vertical section of young disc, somewhat diagrammatic. E, *Cutleria multifida* (Smith) Grev., transverse section of *Aglaozonia*-stage. F, H, *C. adspersa* (Roth) De Not., successive transverse sections near growing margin of gametophyte. *a*, assimilatory hair; *br*, branch; *h*, hair; *m*, meristem; *r*, rhizoid; *t*, compact thallus. (B after Falkenberg; E after Kuckuck; G after Reinke; the rest after Sauvageau.)

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meristems. Uniseriate branches (fig. 52 B, *br*), which arise, as in the trichothallic species of *Ectocarpus* or as in *Elachista*, from the segments below the meristem, add to the number of assimilatory hairs and lead to a progressive broadening of the thallus. The branching of *C. multifida* is due to periodic failure of the filaments to fuse. The gametophytic thalli of Cutleriales are thus produced by congenital fusion of numerous distinct threads which appear as separate entities in and beyond the region of the meristem.

In radial longitudinal (fig. 52 A) or transverse (fig. 52 D) sections through the growing margin of the disc of *Zanardinia* ((23) p. 71, (25) p. 290) the products of the two superposed sets of threads can be traced back for long distances into the compact thallus. The several layers composing the mature plant (fig. 52 C) originate from them by division parallel to the surface (cf. fig. 52 A). The inner segments gradually enlarge, while the outer undergo plentiful anticlinal division. In transverse sections through the margin of the disc (fig. 52 D) the cells are seen to multiply largely by crosswise division, as in many polystichous Ectocarpales. The structure and mode of formation of the thallus of *Cutleria adspersa* (cf. fig. 52 F, H) is almost identical ((25) p. 298). *C. monoica* differs in so far as the assimilatory threads exhibit considerable branching also above the meristem; as a result the apical tufts appear relatively bulky ((32) p. 17). Attachment to the substratum is in both genera effected by a mass of little branched rhizoids growing out from the lower cells ((23) pp. 60, 69, (25) p. 290).

Adventitious branches (fig. 51 F, *ad*), recorded in both genera ((23) pp. 63, 70), originate from surface-cells which grow out into a tuft of assimilatory hairs; these soon acquire intercalary meristems and development proceeds in the way above described.

A cross-section of the mature thallus (fig. 52 C) shows several layers of cells which only differ in the larger size of the internal ones. In *Zanardinia* the upper surface of the disc consists of vertical rows of small cells (figs. 52 G; 53 B).

The gametangia of *Cutleria* ((23) p. 65, (36)) are borne laterally on uniseriate threads which arise in tufts on both surfaces of the thallus and appear as irregularly scattered, dark-coloured excrescences to the naked eye (fig. 51 A). The threads bearing the female gametangia are simple or little branched (fig. 53 A), whilst those bearing the numerous male organs are plentifully branched (fig. 53 G), although occasional male gametangia may arise directly from the superficial cells. In *Zanardinia* the gametangia are situated terminally on simple threads that sprout out from the upper surface (fig. 53 B) and form ill-defined sori.

Both types of gametangia are multiseriate[1] and set free the gametes

[1] According to Yamanouchi (38) the male gametangia of *Cutleria multifida* have 22 tiers of 8 cells, the female 4–7 tiers of 4–8 cells; in *Zanardinia* (39) the male often have more than 30 tiers, each of 8 cells, while the female have 3–9 tiers with 2–4 cells.

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separately from each compartment. The dark-brown female gametangia have relatively few and large compartments (fig. 53 A, *f*), each of which produces a swarmer (ovum; fig. 53 F, *o*) with numerous chromatophores; an eye-spot (*s*) is attached to one of the anterior chromatophores and at this point the two flagella are inserted. The

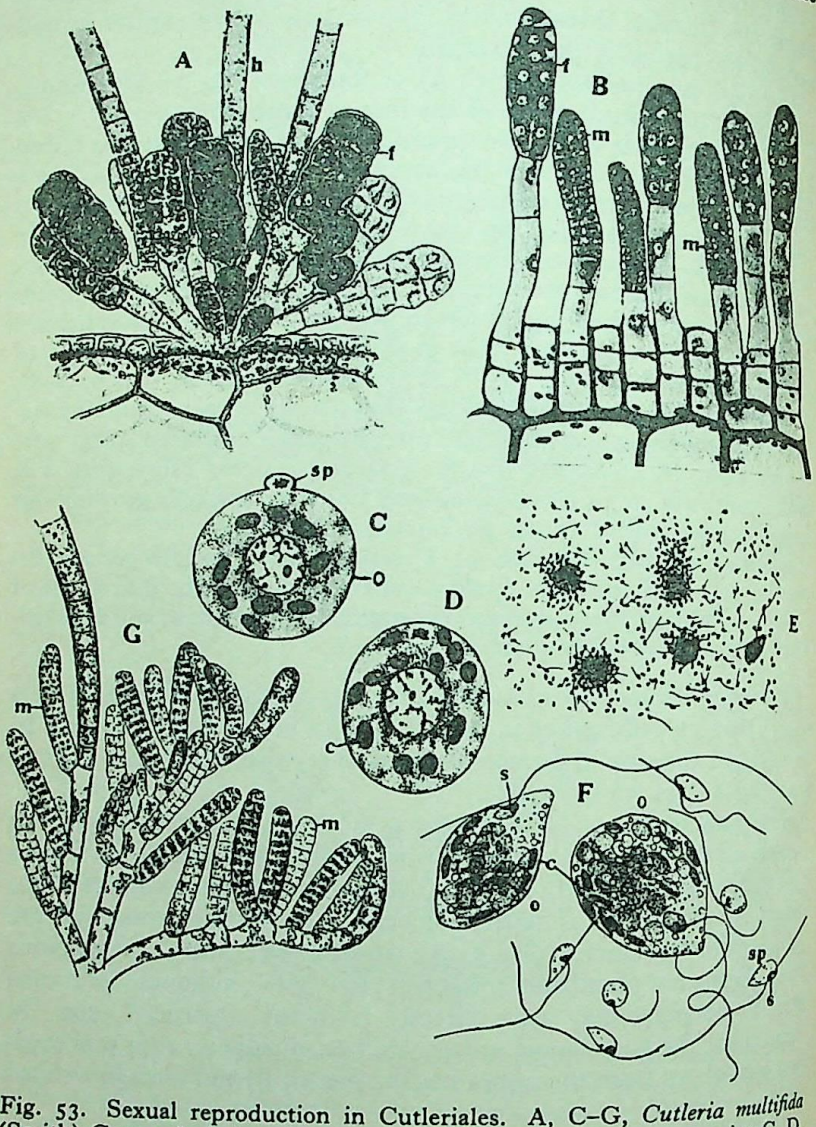

Fig. 53. Sexual reproduction in Cutleriales. A, C–G, *Cutleria multifida* (Smith) Grev.; A, hairs with female, and G with male, gametangia; C, D, two stages in fertilisation; E, fertilisation; F, male and female gametes. B, *Zanardinia collaris* (Ag.) Crouan, part of a sorus of gametangia in section. *c*, chromatophore; *f*, female and *m*, male gametangium; *h*, hair; *o*, female and *sp*, male gamete; *s*, stigma. (A, G after Thuret & Bornet; B after Yamanouchi; the rest after Kuckuck.)

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bright yellow male gametangia possess numerous small chambers, each liberating a minute spermatozoid (fig. 53 F, *sp*), with an eye-spot (*s*) next to the point of insertion of the flagella. Kuckuck ((17) p. 15) states that chromatophores are lacking, but according to Yamanouchi a few small ones are present (cf. also (1) p. 1031).

The female cells soon withdraw their flagella and round off (fig. 53 C, *o*), and in this condition they are fertilised by a male cell (*sp*) which penetrates at the colourless end of the female ((6) p. 424). At the time of fusion the nucleus of the female is in the resting condition, while that of the male shows 22 separate chromosomes ((38) p. 458, (39) p. 13). The secretion of a membrane follows and germination ensues almost immediately.

THE ASEXUAL PHASE

As above mentioned, the zygote of *Zanardinia* gives rise to a diploid asexual plant which is in other respects indistinguishable from the haploid phase and develops in exactly the same way ((39) p. 16). In *Cutleria*, on the other hand, the zygote gives rise to the *Aglaozonia*-stage, as was first established by Falkenberg ((6) p. 427), although the existence of alternation was suspected by Reinke ((23) p. 69). The zygote produces a short erect thread (fig. 51 E, *c*), attached to the substratum by rhizoids (*r*) and later undergoing longitudinal division to form a club-shaped upgrowth, which not uncommonly bears an apical tuft of hairs (fig. 55 B, *h*). This *column* (foot-embryo of Church (2) p. 86), however, remains small and meristematic activity soon becomes restricted to its base (fig. 51 E, *ag*) and results in the formation of a parenchymatous crust (fig. 55 B, *ag*). This is the *Aglaozonia*-stage, which continues to grow by means of a large-celled marginal meristem ((17) p. 15) till it may reach the size of a human hand (fig. 51 G, H). Attachment is effected by a number of septate, little-branched rhizoids (fig. 54 A, *r*).

In *A. parvula* (figs. 52 E; 54 A) the two surfaces are bounded by small cells which enclose 2–3 layers of larger ones. The crusts of *A. melanoidea* ((25) p. 302) are appreciably thicker and there are several rows of small cells on either side. The upper surface bears tufts of hairs which possess the usual basal meristem and are often somewhat sunk (fig. 52 E). Those of *A. parvula* are stated ((16) p. 101) to form linear groups parallel to the direction of growth of the thallus. The dark colour of *A. melanoidea* is, according to Sauvageau ((25) p. 305), due to tannin in the surface-cells.

Both in *Zanardinia* and *Cutleria* (fig. 54 A, G) the unilocular sporangia are formed by tangential division of surface-cells and appear in dense sori on the upper surface. The segment, which grows out to form the sporangium of *Cutleria*, cuts off a basal cell so that the sorus is separated by two layers of cells (fig. 54 A) from the large

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inner ones ((16) p. 102); in *Zanardinia* there are 3–5 of these layers. The nucleus of the sporangium divides successively (fig. 54 E, F), the first divisions being meiotic (fig. 54 B–D). Cleavage ensues only after the full number of nuclei have been formed, and at this stage

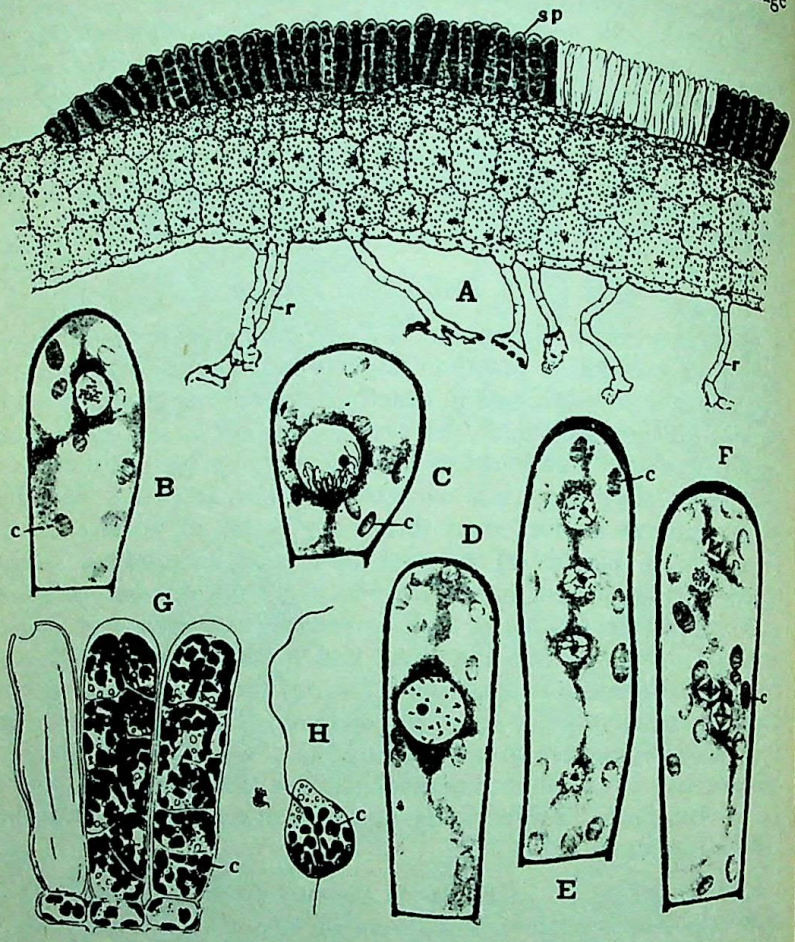

Fig. 54. Asexual reproduction in *Cutleria multifida* (Smith) Grev. A, vertical section of *Aglaozonia*-stage, with a sorus of sporangia; B, uninucleate sporangial initial, formation of nuclear spindle; C, the same, synezesis; D, the same, diakinesis; E, quadrinucleate stage, late telophase; F, metaphase of third nuclear division; G, ripe sporangia, one dehisced; H, swarmer. *c*, chromatophore; *r*, rhizoid; *sp*, sporangium. (A, G, H after Kuckuck; the rest after Yamanouchi.)

the numerous chromatophores are grouped about the individual nuclei. In *Cutleria multifida* usually 8 (sometimes 16 or 32) swarmers are produced, whilst in *Zanardinia* there are only 4 ((39) p. 24).

The zoospores are liberated through an apical aperture formed by gelatinisation of the wall (fig. 54 A, G) and closely resemble the female

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gametes (fig. 54 H). Both in zoospores and gametes Yamanouchi ((39) p. 25) records a row of deeply staining granules connecting nucleus and plasma-membrane, the outermost granule lying at the point of insertion of the flagella.

The zoospores become fixed to a substratum in the way described on p. 118. In *Cutleria multifida* ((16) p. 103) they give rise to an erect thread (fig. 55 F, *e*) attached by one or more branched rhizoids (*r*). The early growth of this thread is probably diffuse, but an intercalary meristem soon arises near its base which cuts off numerous segments on its lower side. These produce successive branches (fig. 55 G, *br*), which exhibit a similar mode of growth, and, as they multiply, become closely apposed to one another. Later, the parts of the threads below the individual meristems coalesce to form a compact cylinder (fig. 55 H, *t*) which bears the free threads as an apical tuft (cf. fig. 51 D). The primary cylinder soon branches and so the mature thallus is gradually established. In *C. adspersa* Sauvageau ((25) p. 322)[1] describes a similar sequence, but here the cylinder widens into a funnel (fig. 51 B) which bears a double row of threads along its margin, a condition very nearly identical with that found in *Zanardinia* (cf. (23) p. 75, (39) p. 28). Later the funnel splits longitudinally (fig. 51 C) to form the mature fan-shaped thallus (fig. 51 I).

THE PROBLEMS PRESENTED BY THE LIFE-CYCLE OF *CUTLERIA* ((13) p. 163)

The life-cycle of *Cutleria* has mainly been investigated at Plymouth (2), Naples (6,23), Heligoland (16), and in the Adriatic (17). Part of the population no doubt follows the cycle described above, although the time of development and of fertility of the two generations of *C. multifida* varies with the geographical location (cf. also (13) p. 165). Thus, at Plymouth, Church ((2) p. 76) found the gametophyte at its maximum in summer (cf. also (14) p. 72) and no longer represented in October, whilst at Naples it occurs chiefly from December to April ((16); cf. also (11) p. 211). The sporophyte is most abundant at Plymouth in October and November and becomes fertile in March and April, whereas at Naples ((16) p. 98) it fructifies in the late autumn. At Heligoland, where the gametophyte is very rare, the *Aglaozonia*-stage is fertile between June and August ((16) p. 100). In the north of England the sporophytic stage is frequent, although the gametophyte is unknown, while on the shores of Scandinavia it is much more abundant and more widely distributed than the latter ((12) p. 17, (18) p. 101, (19) p. 54).

At Plymouth and Naples there is, thus, a certain seasonal sequence between the two phases, the sexual one being represented only during the favourable period of the year, whilst the perennial asexual phase

[1] Based on the germination of parthenogenetic ova (cf. p. 166).

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becomes fertile a few months before the sexual one reaches its maximum; these facts tend to indicate a normal alternation. Schlösser (34) has recently, in cultures undertaken at Naples, grown fertile *Aglaozonia*-plants[1] from the zygotes, while Sauvageau (30) has obtained recognisable sexual plants from the zoospores of the *Aglaozonia*-stage.

Parthenogenetic development of the female cells has frequently been recorded. Germination is rather slow and the products are diverse; sometimes they resemble young *Cutlerias*, sometimes they are more like *Aglaozonias*, and sometimes they are of an intermediate or rudimentary character. A similar diversity has also occasionally been encountered in the products of germination of *Aglaozonia*-zoospores.

In *Cutleria multifida* Reinke ((23) p. 67) and Falkenberg ((6) p. 423) observed sexual fusion only and unfertilised ova failed to exhibit any further development. On the other hand, Thuret ((36) p. 242; cf. also (37) p. 22) and Church ((2) p. 82) record parthenogenetic development only, and both state that in the habitats studied the female plants were in the great majority. The germination-stages obtained by these two investigators were, however, fundamentally different, those of Thuret (from the English Channel) apparently resembling the young filamentous stages of *Cutleria*, whilst those of Church were young *Aglaozonias* (cf. also (17), (25) p. 347). Parthenogenetic development is also recorded by Crouan (3) from Brest and by Derbès and Solier ((5) p. 60) from Marseilles. It has likewise been observed in *Zanardinia* ((39) p. 17), although only early stages of germination were obtained.

Comparable data are available for *Cutleria adspersa*. The male and female gametophytes are widely distributed and equally common in the Mediterranean, although the corresponding *Aglaozonia*-stage has been found only in one or two localities ((25) p. 354). Janczewski ((11) p. 212) found that the female cells germinated only after fertilisation and that they gave rise to young *Aglaozonia*-stages. Sauvageau, on the other hand, both in the Mediterranean (29) and in the Bay of Biscay ((25) p. 312), where male plants are more abundant than female, failed to obtain sexual fusion; the ova in his cultures, however, likewise developed into recognisable *Aglaozonia*-stages ((25) p. 335). The numerous germlings found on the mature thalli of the gametophyte in nature (cf. also (31)) were partly *Aglaozonias* and partly young *Cutlerias* (fig. 55 C), while a few were of the filamentous type to be described below ("forma Church"). Sauvageau concludes that all these had probably developed without sexual fusion, although the possibility of some being derived from fertilised ova is discussed.

The faculty of the female cells to develop apogamously clearly varies. Schlösser (34) was able to stimulate unfertilised ova to further development by treatment with various chemicals and by centrifuging; the resulting plants produced oogonia. If strong centrifugal force was applied during the first division of such ova, sterile *Aglaozonia*-stages

[1] The species is not stated.

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resulted; these are suspected of being diploid, but for this there is at present no cytological proof.

Church ((2) p. 89) found that many of the zoospores of the *Aglaozonia*-stages of *C. multifida* developed into branched upright filaments, longitudinally divided in their lower part and bearing antheridia, a form already encountered by Kuckuck ((15) p. 251) and described by him as var. *confervoides*. It is strange, in view of the scarcity of male plants at Plymouth, that Church obtained only antheridia in these cultural forms. This may indicate a dimorphism of the two sexes under certain conditions in nature (cf. also (13) pp. 166, 178). In some of Church's filamentous stages (fig. 55 I) the lower part broadened into a small *Aglaozonia* (*ag*) and such germlings are usually described as the "forma Church" ((25) p. 329). Kuckuck (16) at Heligoland obtained from *Aglaozonia*-zoospores recognisable female *Cutleria*-plants, as well as the confervoid type and the "forma Church", in this instance with oogonia (fig. 55 I, *f*). The zoospores of *A. melanoidea* (27, 30) afford in cultures mainly filamentous *Cutleria*-stages, but also a few *Aglaozonia*-forms, while those of *A. chilosa* have produced confervoid stages with oogonia, as well as the "forma Church" (33).

The considerable diversity in the products of germination of parthenogenetic ova and zoospores is not easily elucidated. The filamentous forms obtained by Church and others from zoospores may well be cultural stages of the normal dioecious gametophyte; they recall the precociously fertile sporophytic stages met with in diverse Ectocarpales under conditions of culture. On the other hand parthenogenetic ova produce not only fresh gametophytes,[1] but evidently rather more frequently *Aglaozonia*-stages which must presumably be haploid. Zoospores can seemingly also produce such stages, which then arise as a vegetative outgrowth from the base of the primary filament ("forma Church", fig. 55 I); this likewise suggests the existence of haploid *Aglaozonia*-individuals. The probable occurrence of many haploid *Aglaozonias* in nature, presumably originating in the first place by apogamous development of female cells, has been strengthened by Sauvageau's observations ((32) p. 21) on *Cutleria monoica*. An apogamously produced plant of *Aglaozonia chilosa* was observed to give rise (fig. 55 E) by vegetative proliferation to new *Cutleria*-plants (*g*).

A survey of the facts ((41) p. 406) indicates that, side by side with a normal alternation, there is in many regions extensive apogamous development of the female cells, which results for the most part in the production of haploid *Aglaozonia*-individuals. In diverse localities, in fact, it would appear as though the majority of these stages may be haploid and that these possibly propagate themselves indefinitely by haploid zoospores. At the same time, however, the female cells and the swarmers of the haploid *Aglaozonias* can evidently also give rise

[1] Since the *Aglaozonia*-stage of *C. adspersa* is rare in the Mediterranean, a direct multiplication of this species by parthenogenetic ova is possible.

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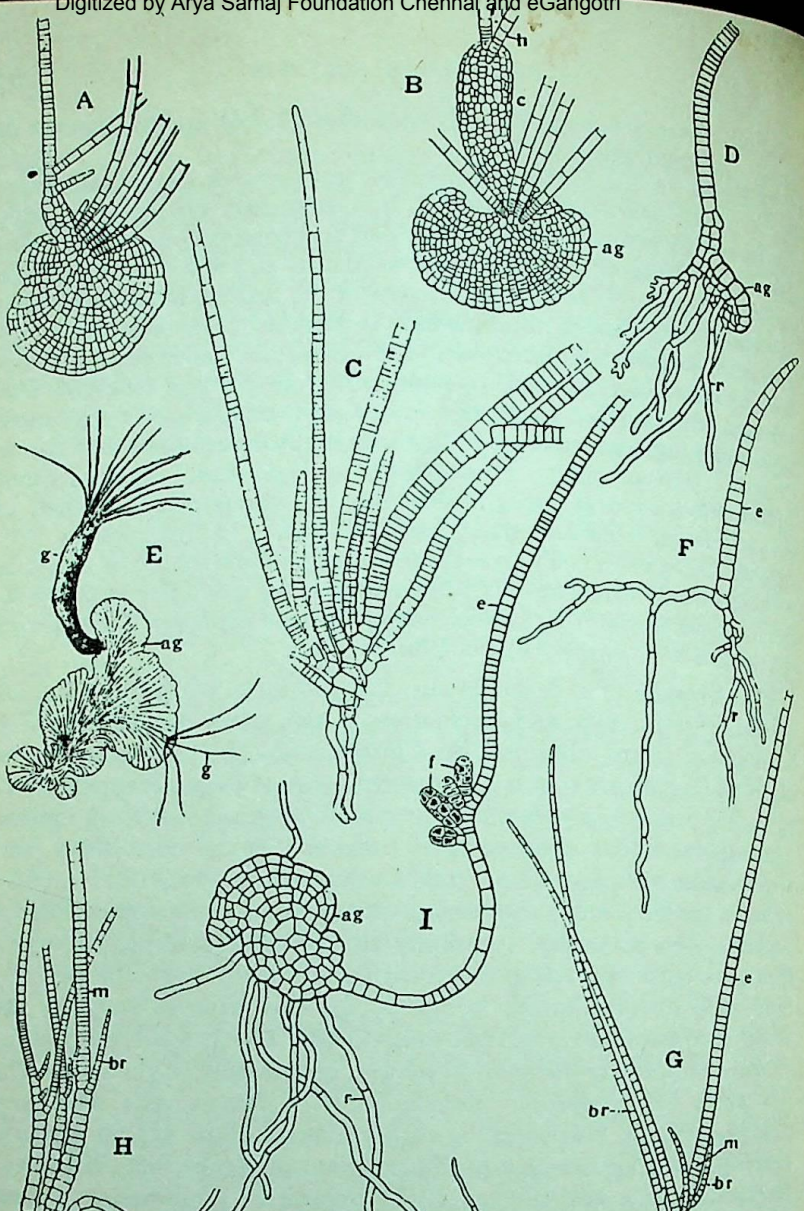

Fig. 55. Diverse developmental stages of Cutleriales. A, C, *Cutleria adspersa* (Roth) De Not.; B, D, F–I, *C. multifida* (Smith) Grev.; E, *C. monoica* Olliv. A, I, the "forma Church", in I with oogonia (*f*); B, D, young *Aglaozonia*-stages; C, forma Thuret (early stage of gametophyte); E, production of gametophyte from *Aglaozonia*-stage; F–H, early stages in development of gametophyte. *ag*, *Aglaozonia*-stage; *br*, branch; *c*, column of *Aglaozonia*-stage; *e*, erect thread; *g*, gametophyte; *h*, hair; *m*, meristem; *r*, rhizoid; *t*, compact region of thallus. (D, F–I after Kuckuck; the rest after Sauvageau.)

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to sexual plants. The actual state of affairs can probably only be settled by an extensive cytological study of *Aglaozonias* in different regions. How far the production of *Cutleria*-stages from haploid *Aglaozonia*-plants by vegetative means is a widely distributed phenomenon, as Sauvageau ((32) p. 25, (33)) evidently believes, remains to be seen.

THE AFFINITIES OF CUTLERIALES

The mode of development of the thallus in Cutleriales shows analogies with that seen in Elachistaceae (p. 68). In view, however, of the probable simple filamentous nature of the gametophyte in the latter, the resemblance in vegetative features is unlikely to imply any close affinity. So far as present evidence goes, the Cutleriales must be regarded as a direct development from the primitive heterotrichous ectocarpoid stock with its trichothallic growth, isomorphic alternation, and marked tendency towards oogamy (p. 122). Sauvageau ((25) pp. 306, 356, (26)), laying special stress on the *Aglaozonia*-stage which presents many points of resemblance to certain *Zonarias* (p. 308), believes in an affinity with Dictyotales.

There can be little doubt that alternation in this order is primarily isomorphic ((8) p. 245, (41)). The appearance of an *Aglaozonia*-crust as a basal outgrowth from a gametophytic filament in the "forma Church" (fig. 55 I), usually after the latter has undergone longitudinal septation in its lower part, suggests that the column of the normal *Aglaozonia* is an arrested and sterile structure, homologous with the *Cutleria*-thallus. Sauvageau ((25) p. 330) has, in fact, pointed out that in the "forma Church" the *Cutleria*-threads are often borne at the apex of a short, but evident column. The typical sporophyte shows a clear derivation from a heterotrichous ancestry, the column representing the erect, the crust the prostrate system. The fact that the latter is here formed secondarily does not appear to be of significance. The gametophyte, on the other hand, shows no trace of heterotrichy. It is possibly this dominance of the erect system that leads also in *Aglaozonia* to the primary formation of an upright growth. It is to be noted that the two generations of *Zanardinia* and the *Cutleria*-gametophyte exhibit the trichothallic growth characteristic of many of the specialised members of Ectocarpales (cf. also Sporochnales), whereas the *Aglaozonia*-crusts show the marginal (apical) growth which is invariably met with in the prostrate system.

The instances discovered by Sauvageau, in which new *Cutleria*-plants arise vegetatively from the *Aglaozonia*-stage of *C. monoica* (cf. fig. 55 E), illustrate the presence of both parts of the heterotrichous system in what is to all intents and purposes a single individual. They possibly afford a picture of the ancestral condition when the alternation in *Cutleria* was an isomorphic one between two heterotrichous

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individuals, neither system of which necessarily showed the specialisation seen in the present-day forms. In the course of further evolution the sexual individual lost the prostrate and the asexual one the upright system, except for the relic preserved in the shape of the column.

Such an interpretation explains *inter alia* the frequent association of gametophytic threads bearing sex organs with a prostrate *Aglaozonia*-crust ("forma Church", fig. 55 I). This condition is evidently not confined only to the precociously fertile gametophytic stages, since, according to Gran ((9) p. 25), *Aglaozonia*-stages can arise from young *Cutlerias* which already show definite coalescence of threads. The view that the heteromorphic alternation of *Cutleria* is derived from an isomorphic one accords with the occurrence of strict isomorphic alternation in *Zanardinia*. Young plants of the latter show many resemblances to the early stages of development of *C. adspersa* ((25) p. 289).

Oltmanns ((21) p. 120) looks upon the *Aglaozonia*-stage as a new structure originating from the base of the *Cutleria*-plant and to which the production of unilocular sporangia was gradually relegated. This necessitates the assumption that at one time asexual organs were borne upon the *Cutleria*-plant itself; since they occur on identical individuals in *Zanardinia*, this is quite plausible. The Cutleriales are, however, clearly related to the Ectocarpales with their marked heterotrichy, and it seems far more likely that the *Aglaozonia*-stage represents a further development of an ancestral prostrate system than that it is a new structure. An elaborate development of the prostrate system at the expense of the upright one is well shown also in other series of Phaeophyceae (cf. Sphacelariales, p. 281).

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Order IV. *SPOROCHNALES*

The members of this order (1) are distinguished by the possession of highly organised sporophytes which bear unilocular sporangia only. Their zoospores give rise to minute ectocarpoid gametophytes bearing antheridia and oogonia (15-17). Although sexual fusion has not yet been observed, its occurrence in nature can scarcely be doubted, especially in regions favourable to the development of these plants. The Sporochnales thus show heteromorphic alternation combined with oogamy and this, no less than the peculiar characteristics of the sporophyte, warrant their being regarded as a distinct order. The few genera, included in the single family Sporochnaceae, apparently have their chief centre of distribution in the Southern Hemisphere, although a number of species are widely distributed in warmer seas; *Sporochnus pedunculatus* (fig. 56 A) and *Carpomitra costata* (Stackh.) Batt. (*C. Cabrerae* Kütz.; fig. 56 D) are rare British seaweeds.

Bellotia, *Encyothalia*, and *Perithalia* are known only from Australia and the adjacent islands, and this is true also of a considerable number

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of the species of the other genera. A few species of *Nereia* occur in the Mediterranean and on the west coast of Africa, while those of *Carpomitra* are found on the western shores of Europe, on the Pacific coast

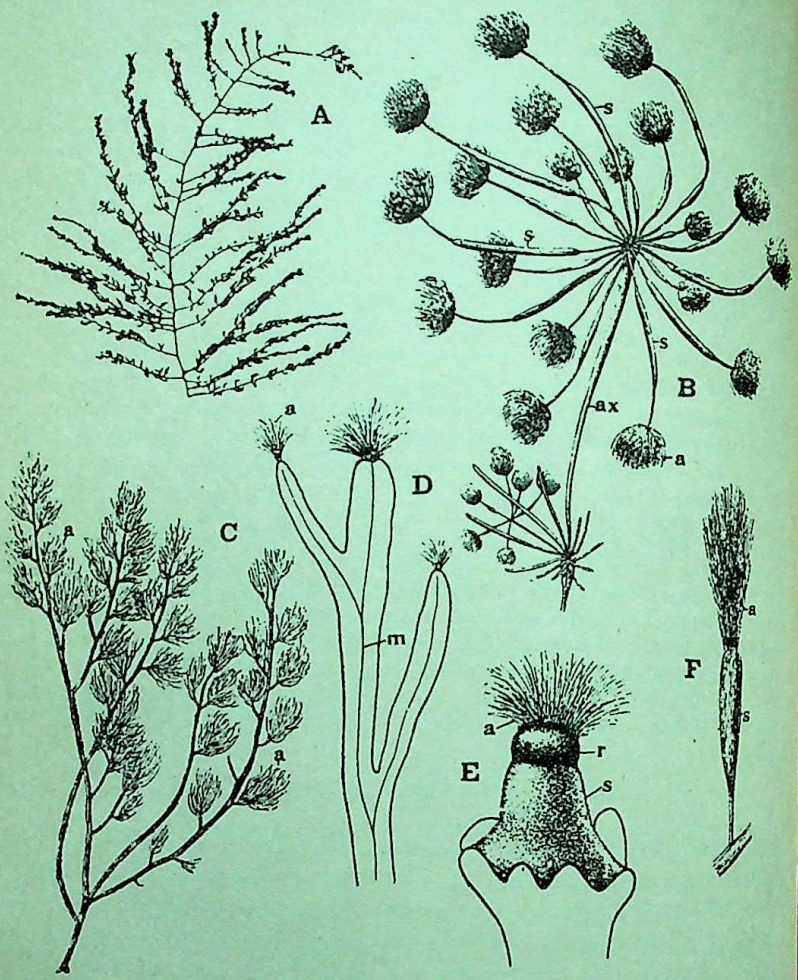

Fig. 56. Habits of Sporochnales. A, F, *Sporochnus pedunculatus* (Huds.) Ag.; A, part of a plant; F, fertile lateral. B, *Bellotia eriophorum* Harv., part of a fertile plant. C, *Nereia filiformis* (J. Ag.) Zanard. D, E, *Carpomitra costata* (Stackh.) Batt.; D, small part of thallus; E, fertile tip enlarged. *a*, assimilatory threads; *ax*, principal axis; *m*, midrib; *r* (in E), annular swelling above sorus; *s*, sorus. (A, photo: R. Cullen; B after Harvey; C after Kützing; D, E after Sauvageau; F after Kjellman.)

of North America, in South Africa, and Australasia. *Sporochnus* is represented in the Australian seas and on the west coasts of Europe, *S. pedunculatus* occurring as far north as Scandinavia. Certain species found in the Northern Hemisphere possibly owe their presence there

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to transport on ships' bottoms. All Sporochnaceae tend to grow below low-tide level, often in deeper water.

THE SPOROPHYTE

The members of this order are moderately large seaweeds, characterised by the fact that the apices of all the branches of a growing plant are crowned by a tuft of free, unbranched assimilatory hairs (figs. 56 B, D, E; 57, *a*). Each of these lengthens with the help of a basal or suprabasal meristem, but these meristems take no part in the growth of the actual thallus below. *Sporochnus pedunculatus* ((4) pl. 56, (19) p. 35; fig. 56 A) is a short-lived annual ((10) p. 71; (11) p. 444), with well-branched cylindrical axes, up to 45 cm. in length and bearing numerous branchlets of limited growth, each of which terminates in such a tuft of hairs (fig. 56 F).

Encyothalia ((6) pl. 62, (9) p. 238) has a similar habit. *Nereia filiformis* ((3) p. 57, (19) p. 67; fig. 56 C) is less richly branched; the laterals of limited growth are here not always so clearly defined, while the apical tufts of hairs are particularly strongly developed. In *Bellotia eriophorum* ((5), (6) pl. 69, (7) p. 288, (9) p. 238; fig. 56 B), recorded from New Holland and Tasmania, the elongate laterals of limited growth arise in whorls. A rather different habit is seen in *Carpomitra costata* ((4) pl. 14; fig. 56 D), in which all the branches of the irregularly dichotomous thallus are flattened and provided with a broad midrib (*m*); there are no laterals of limited growth.

The various genera are specially distinguished by the positions of the sori. In *Nereia* these show no very definite location and are not always conspicuous, although they tend to develop on or near the shorter branches ((12) p. 77). The sori of *Bellotia* (fig. 56 B, *s*) and *Encyothalia* constitute swollen regions in the middle of the laterals. In *Sporochnus* ((8) p. 137) they likewise develop on the laterals, occupying a longer or shorter stretch just beneath the tuft of assimilatory hairs so that such fertile laterals appear as stalked pear-shaped structures (fig. 56 F, *s*). The sori of *Carpomitra* (fig. 56 E, *s*), lastly, are differentiated at the tips of the branches beneath the apical hairs, from which they are separated by an annular swelling (*r*) ((14) p. 147).

Longitudinal sections (fig. 57) of the mature thalli appear to show considerable uniformity. They exhibit a number of longitudinal rows of cells which in *Carpomitra* are sometimes slightly twisted ((14) p. 169); the central cells (fig. 57, *mr*) are elongate and colourless, while the peripheral ones (*c*) are shorter and packed with discoid chromatophores. In *Nereia* (fig. 57 A) the surface-layer bears densely aggregated 2–3-celled paraphyses (*p*), but in the other genera similar outgrowths are only produced in the fertile regions. The mature thallus is formed from a horizontal meristem (*m*) which lies beneath the tuft of assimilatory hairs (*a*). Its mode of origin will be best understood

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from a description of the early stages in development which are known only for the European genera ((12), (13) p. 46, (14), (17)).

The young plants, produced from the gametophytes, at first consist of a simple erect thread with diffuse growth, the *proembryo* of Sauvageau ((14) p. 157; fig. 58 F, H, K, *e*); this is anchored to the substratum by rhizoids (*r*). The proembryo soon becomes differentiated into three regions. The lower part, comprising a row of often narrower cells, constitutes a pedicel which in *Carpomitra* is of some

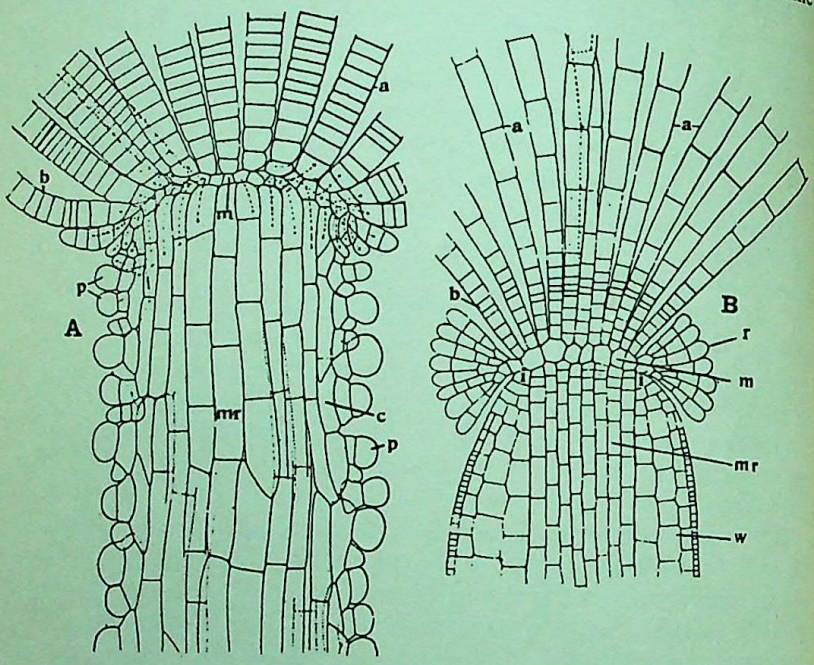

Fig. 57. Structure of Sporochnales. A, *Nereia filiformis* (J. Ag.) Zanard., longitudinal section of growing region of practically mature plant (after Kuckuck). B, *Carpomitra costata* (Stackh.) Batt., longitudinal section through apex, diagrammatic (after Sauvageau). *a*, assimilatory thread; *b*, meristem of same; *c*, cortex; *i*, initial cell of wing of thallus; *m*, meristem of thallus; *mr*, medullary threads (midrib in B); *p*, paraphyses; *r* (in B), annular swelling; *w*, wing.

length (fig. 58 I, *p*), although relatively short in *Nereia* (fig. 58 A–C, *p*); this region plays no further part in the development of the mature thallus. The upper part differentiates a basal meristem (*me*) and constitutes the first hair of the future tuft (*a*, *a1* in fig. 58 A–C, I, J). The single flat cell (fig. 58 I, *m*), situated between these two regions, is destined to give rise to the meristem from which the mature thallus is produced.

The cell in question (fig. 58 A–C, J, *b1*, *b2*) undergoes longitudinal division in various planes to form a progressively broadening meri-

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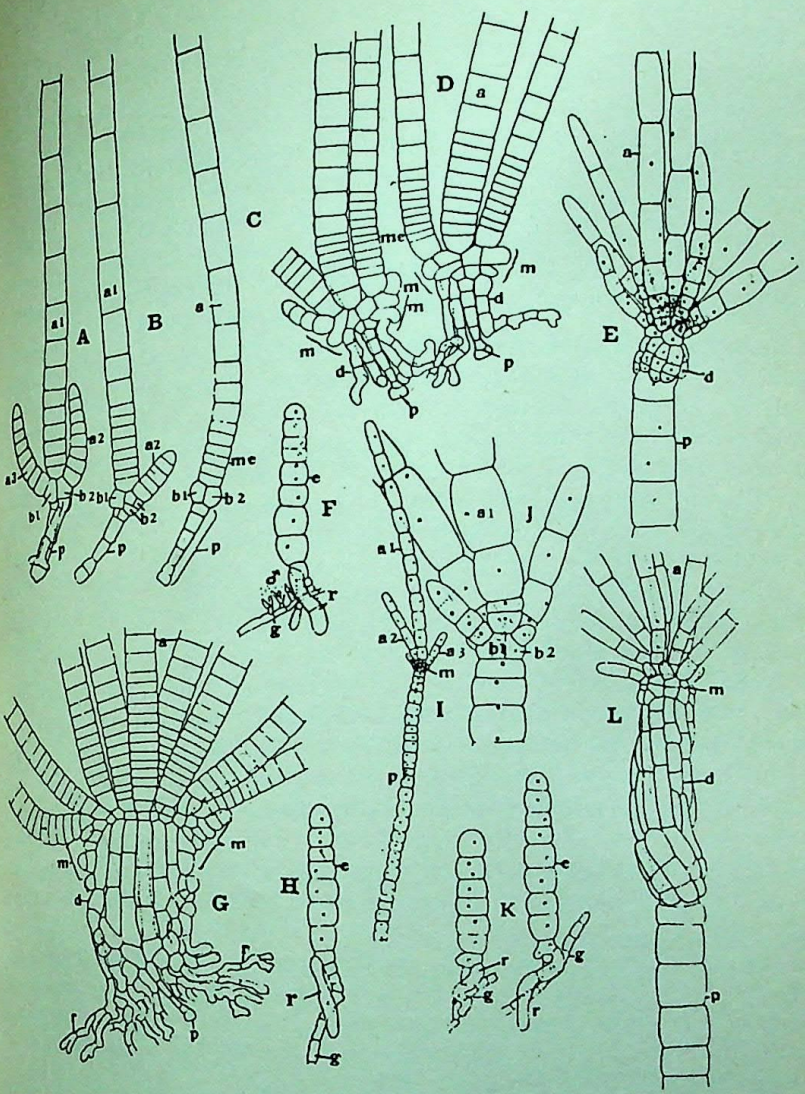

Fig. 58. Development of the thallus in Sporochnales. A–D, G, *Nereia filiformis* (J. Ag.) Zanard. (after Kuckuck); A–C, three germlings; D, two older plants, showing commencing formation of downgrowing threads; G, older plant with rhizoids. E, F, H–L, *Carpomitra costata* (Stackh.) Batt. (after Sauvageau); E, L, formation of downgrowing threads; F, H, K, diverse young proembryos attached to the gametophyte; I, J, parts of two proembryos showing formation of the meristem. *a*, *a* 1, *a* 2, etc., assimilatory threads; *b* 1, *b* 2, cells formed by septation of primary meristematic cell; *d*, downwardly growing threads; *e*, proembryo; *g*, gametophyte; *m*, meristematic plate of thallus; *me*, meristem of assimilatory hair; *p*, pedicel; *r*, rhizoid.

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stematic plate (cf. figs. 58 D, G; 57 A, *m*). Both before and during the septation of the primary meristematic cell, successive protuberances arise on the upper side and gradually develop into further assimilatory hairs (fig. 58 A, B, *a2*, *a3*); the later ones originate from the individual units of the meristem as it broadens. Each cell of the meristem also gives rise on its lower side to an outgrowth (fig. 58 D, E, L, *d*), which lengthens into a downwardly growing multicellular thread. The individual threads thus produced coalesce to form a multicellular pseudo-parenchymatous body (fig. 58 G), which is the beginning of the future thallus and is intercalated (fig. 58 L) between the pedicel (*p*) and the apical tuft (*a*). Church ((2) p. 39) quite unwarrantably speaks of a parenchymatous organisation.

It is not altogether clear how long the addition of further threads from the margin of the meristem continues. According to Sauvageau ((14) p. 171) only a limited number are produced in *Carpomitra*, and further widening of the thallus takes place by periclinal divisions in the threads, accompanied by a corresponding division in the cells of the meristem. Continued lengthening of the rows of cells thus produced is effected by horizontal division of the meristematic cells. The pedicel undergoes no further change and merely serves to raise the embryo above the substratum. Sooner or later the cells at the base of the young thallus grow out into bifurcating rhizoids (fig. 58 G, *r*) which gradually hide the pedicel and spread out upon the substratum.

According to Sauvageau ((14) p. 179) only the midrib of *Carpomitra* (fig. 57 B, *mr*) arises in this way, the wings (*w*) being formed by periclinal division of the segments of an initial cell (*i*), recognisable just below the meristem (*m*) and regarded as a reflexed marginal cell of the latter. Another distinctive feature of this genus lies in the development, from the margin of the meristem, of a horizontal tuft of coalesced threads with enlarged distal cells (fig. 57 B, *r*) that ultimately gives rise to the marked annular swelling situated just below the apical tuft (fig. 56 E, *r*).

Few details are available as to the mode of formation of the branches. Judging by a figure given by Kuckuck ((12) p. 76) for *Nereia*, it would seem that branches arise by cessation of division in a part of the meristem, the two portions thus segregated developing respectively as a continuation of the main axis and as a branch.

In the richly branched genera the numerous groups of assimilatory hairs must constitute an important photosynthetic system, and it is significant that, in *Carpomitra* and *Sporochnus*, the sori are located in their immediate neighbourhood. These tufts of threads, so similar to those found in *Elachista* and in Cutleriales, here play no part at all in the growth of the thallus, which is produced entirely from the separate meristem arising from an intermediate cell of the proembryo. It is indeed difficult to find a parallel among other Brown Algae for the peculiar mode of thallus-development obtaining in the Sporochnales.

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The position of the sori has already been mentioned. In *Nereia* ((12) p. 77) the small sporangia (fig. 59 A, *u*) arise either from the peripheral cells that bear the paraphyses (*p*) or from the basal cells of the latter; the dilated end-cells of the paraphyses form a protective covering. In the remaining genera the sporangia are borne on special fertile threads that grow out from the surface-cells only in the region of the sori. The fertile threads of *Sporochnus* (fig. 59 B) and *Carpomitra* (fig. 59 G) are branched, with enlarged terminal cells, and bear the several sporangia (*u*) laterally. Those of *Bellotia* are elongate and often unbranched. The sporangia open by a broad apical rupture (fig. 59 B, G, *d*). The zoospores appear to be of the usual pattern (fig. 59 J); Sauvageau describes those of *Carpomitra* as having a single posterior chromatophore provided with an eye-spot.

THE GAMETOPHYTE

The gametophytes of *Carpomitra* (14, 15) were discovered in 1926 by Sauvageau; a year later he described those of *Nereia filiformis* (16, 17), and subsequently also those of *Sporochnus pedunculatus* ((18) p. 122), although of the last only sterile prothalli have so far been found. Germination of the zoospores (fig. 59 E) takes place in the way described on p. 118, the contents of the embryospore passing into a protuberance which divides further to form the gametophyte. In *Carpomitra* and *Sporochnus* the cells of the resulting prothalli each possess only a single parietal much dissected chromatophore (fig. 59 F), which contrasts with the numerous discoid chromatophores found in those of the sporophyte.

The prothalli are always ectocarpoid in form (fig. 59 C); those of *Nereia* are usually dioecious, while those of *Carpomitra* (fig. 59 I) are monoecious. In the latter the antheridia (*an*) are one-celled and generally form terminal clusters on the ultimate branches. The well-branched male prothalli of *Nereia* (fig. 59 D) bear the numerous small, conical antheridia (*an*) in a lateral or terminal position upon the upper cells; the antheridia are here two-celled and each compartment opens separately to the exterior. In both genera the male organs are colourless and composed of uninucleate cells. There can be little doubt that each cell forms a single spermatozoid, although these have not so far been observed.

The female organs, which give rise to the proembryos by transverse division, are in *Carpomitra* enlarged terminal cells of elongate laterals (fig. 59 I, *f*); in *Nereia* they occupy the apices of the unbranched female prothalli (fig. 59 H). So far only apogamous development of the female cells, without liberation of an ovum, has been observed. In view of the production of numerous antheridia from which the contents are liberated, it is probable that fertilisation sometimes occurs in nature. On the other hand, as Sauvageau ((14) p. 185) points out,

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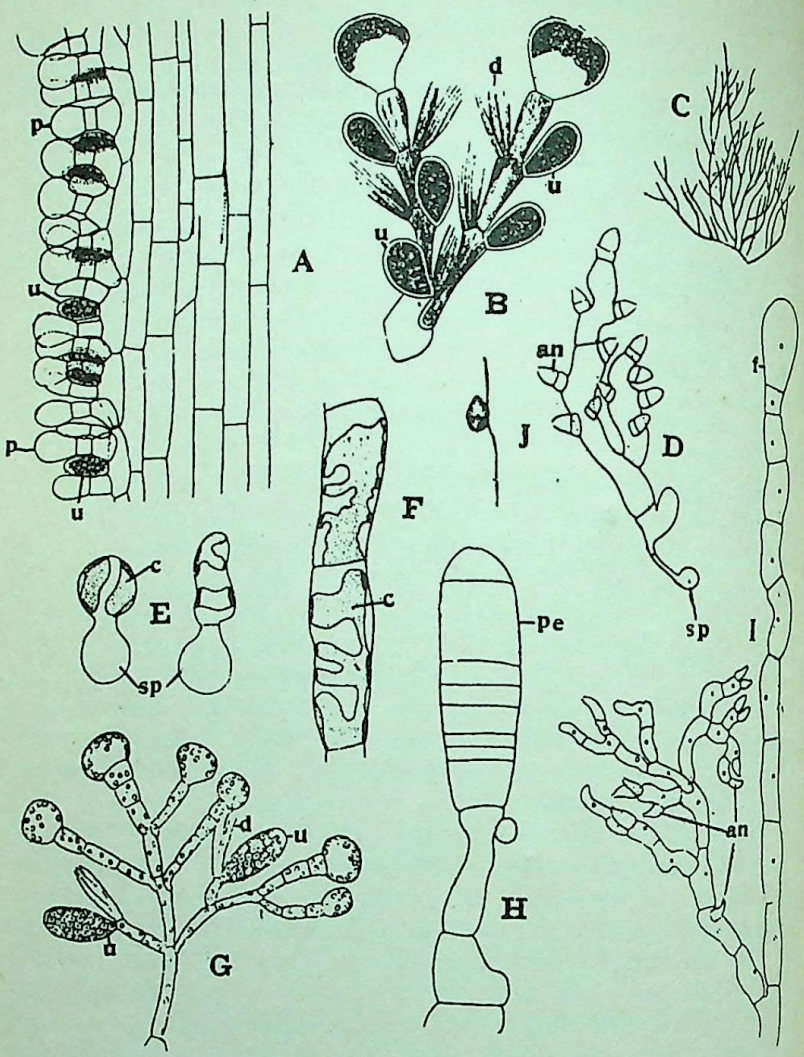

Fig. 59. Reproduction of Sporochnales. A, D, H, *Nereia filiformis* (J. Ag.) Zanard.; A, longitudinal section of part of thallus, with sorus; D, young male gametophyte; H, female gametophyte, with proembryo (*pe*). B, J, *Sporochnus pedunculatus* (Huds.) Ag.; B, sporangium-bearing thread; J, zoospore. C, E–G, I, *Carpomitra costata* (Stackh.) Batt.; C, diagrammatic representation of gametophyte; E, germinating spores; F, two cells of the gametophyte; G, sporangium-bearing thread; I, part of prothallus, with male and female branches. *an*, antheridium; *c*, chromatophore; *d*, dehisced sporangium; *f*, female cell (?); *p*, paraphyses; *sp*, spore; *u*, unilocular sporangium. (A after Kuckuck; B after Kjellman; J after Johnson; the rest after Sauvageau.)

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it is possible that the inflated terminal cells are not actually oogonia, but merely cells of the gametophyte giving rise vegetatively to a new sporophyte. The numerous antheridia, which are evidently functional, would be difficult to explain if this were so. The single chromatophore of *Carpomitra* gradually breaks up into numerous discs as the proembryo develops.

AFFINITIES OF THE SPOROCHNALES

The Sporochnales constitute a highly specialised group of uncertain affinity. As regards the characters of the sporophyte they stand altogether isolated, while the gametophytes show resemblances to those of Desmarestiales and Laminariales. The unicellular antheridia of *Carpomitra*, with their colourless contents, are remarkably like those of the latter order, and there is also similarity in the position of the supposed oogonia. The two-celled antheridia of *Nereia* possibly indicate a stage in reduction from the plurilocular type. It is significant of the specialisation of the sporophyte that all indications of heterotrichy have disappeared.

Berthold ((13) p. 48) assumed a relationship with Mesogloeaceae, whilst Oltmanns refers especially to *Myriogloea* (p. 85). It is difficult to detect any real affinity with either, since the mode of formation of the thallus in Sporochnales is quite unique. A certain intercalary cell of the erect filamentous proembryo divides to form the horizontal meristem from which the mature thallus arises as a system of downwardly growing threads. This to some extent recalls the condition in *Desmarestia*, where the bulk of the thallus is produced from downwardly growing cortical threads, although these here arise at diverse points along the uniseriate main axis. The analogy is heightened in certain instances observed by Sauvageau ((14) p. 167) in *Carpomitra*, in which more than one transverse meristem arises in the course of a proembryonal thread.

Literature of Sporochnales

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Order V. *DESMARESTIALES*

The three genera included in this order possess sporophytes showing considerable anatomical specialisation. *Desmarestia* is a widely distributed lithophyte in the colder seas of both hemispheres. The common British species, *D. viridis* (Müll.) Lamour. ((9) pl. 312) and *D. aculeata* (L.) Lamour. ((9) pl. 49; fig. 60 A), occur on the Atlantic shores of Europe and North America, extending north to Greenland ((26) p. 857), although they are absent from the Mediterranean. The genus is well represented on the western shores of North America (from Behring Island to Southern California), and Setchell and Gardner ((31) p. 245, (32) p. 559) distinguish a considerable number of species, of which only *D. ligulata* ((9) pl. 115; fig. 60 C) is also recorded from the Atlantic.[1] Another group of species, in part with large thalli, occur in the Antarctic ((5) p. 149, (8) p. 36, (24) p. 182, (33) p. 16), while the monotypic *Phaeurus* is known only from the latter region. *Arthrocladia*, with the single species *A. villosa* ((9) pl. 64; fig. 60 D), is found on most European shores (incl. the Mediterranean), as well as on the Atlantic coasts of North America. The Desmarestiales, though sometimes found near low-tide level, usually inhabit the sublittoral region ((2) p. 767, (14) p. 262, (19) p. 73, (21) p. 384), often extending to some depth; in the Antarctic they play a dominant rôle in the sublittoral vegetation ((24), (33) p. 255), the most conspicuous species being *D. compressa* and *D. anceps* Mont.

Arthrocladia, as well as certain *Desmarestias* (*D. viridis*, *D. ligulata*), are annuals, but other species of the latter survive for more than one year. Thus, in the European *D. aculeata* (fig. 60 A) the older portions of the thalli persist through the winter and give rise to numerous fresh shoots in the early part of the next season ((23) p. 175, (35) p. 7). The plants always bear unilocular sporangia only,[2] and the zoospores of *D. aculeata* have been shown (30) to give rise to minute filamentous prothalli producing oogonia and antheridia (fig. 62 J, K) and closely resembling those of Laminariales. The zoospores of *Arthrocladia* (28) also develop into ectocarpoid growths, but these have so far exhibited only an apogamous production of sporophytes.

[1] Also reported from New Zealand ((10) p. 217).

[2] The plurilocular sporangia recorded by Okamura ((20) pl. 38) in *Desmarestia tabacoides* are probably a result of confusion with an epiphyte (cf. (22) p. 325).

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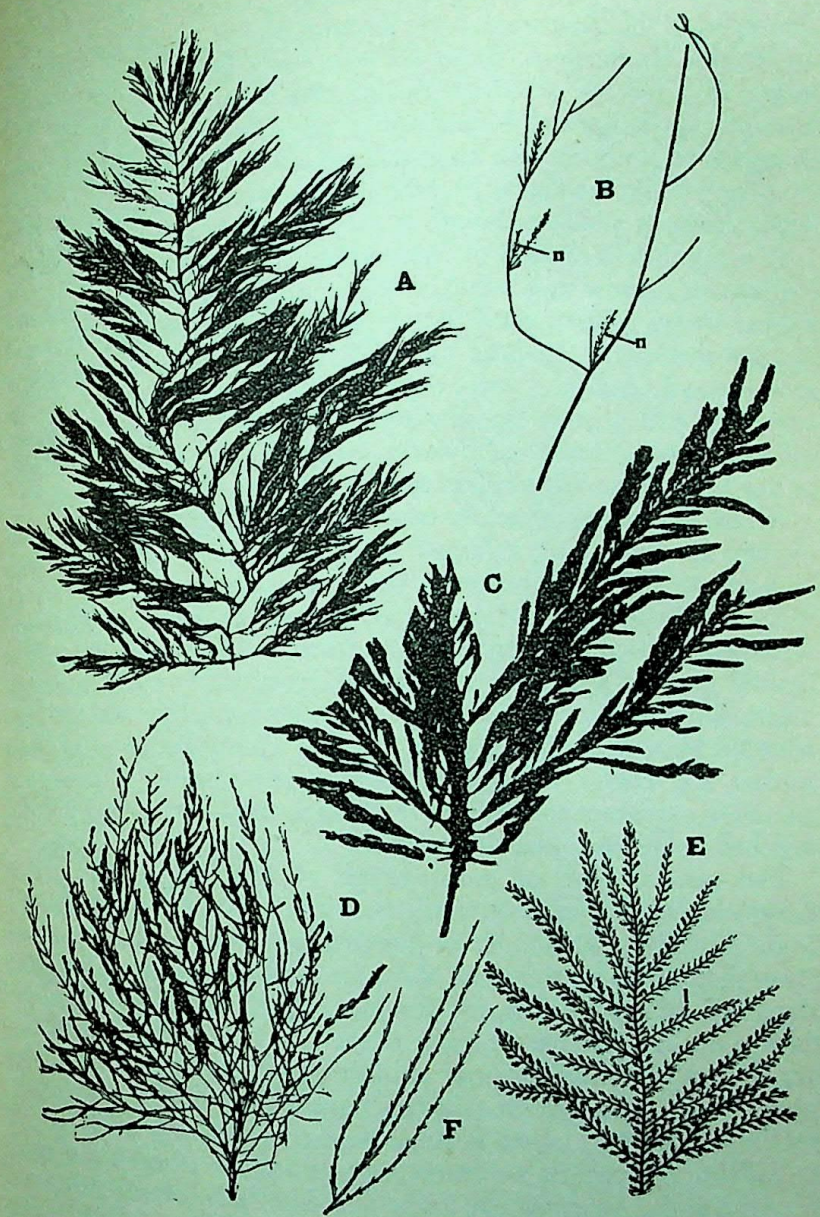

Fig. 60. Habits of Desmarestiales. A, B, E, F, *Desmarestia aculeata* (L.) Lamour.; B, origin of new shoots (*n*) on last year's plant; E, small part showing the laterals (*l*) of limited growth; F, winter condition. C, *D. ligulata* Lamour., part of a plant. D, *Arthrocladia villosa* (Huds.) Duby. (B after Söderström; E after Newton; F after Taylor; the rest photos: R. Cullen.)

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STRUCTURE OF THE SPOROPHYTE

The species of *Desmarestia* are usually richly branched plants of appreciable dimensions. Thus, *D. aculeata* (fig. 60 A) may reach a length of 2 metres, although the annual *D. viridis* is smaller. The Antarctic *D. compressa* Reinsch may grow to 3 metres ((34) p. 19), *D. anceps* to 4 metres with an attaching disc up to 20 cm. in diameter ((8) p. 40), while the Pacific *D. herbacea* reaches 2½ metres ((32) p. 567). *Arthrocladia* is smaller, though it may be nearly a metre in length.

In a number of species of *Desmarestia* the diverse branches of the thallus are narrow and subcylindrical,[1] although the principal axes appear always to show some flattening (cf. fig. 61 D). In the so-called ligulate species (*D. ligulata*, fig. 60 C; *D. herbacea*) this flattening is more pronounced, and most of the branches are developed as leafy expanses with dentate margins and often with more or less clearly marked midribs; there is, however, always a short cylindrical portion at the base of the whole plant and at the base of each branch.

All the branching generally takes place in one plane and the longer laterals are commonly arranged in opposite pairs (fig. 60 C, left); *D. aculeata* (fig. 60 E), however, shows alternate branching ((35) p. 4). A characteristic feature of the growing plants, both in *Desmarestia* and *Arthrocladia*, is the presence of numerous, richly branched laterals of limited growth, appearing as short feathery tufts to the naked eye. These are distichously arranged in *Desmarestia* (fig. 60 E, *l*) and whorled in *Arthrocladia* (fig. 60 D). In *Phaeurus* ((34) p. 24) these laterals are coarse, unbranched structures forming a dense and relatively persistent covering to the longer axes. The thalli are usually attached by a broad discoid holdfast.

The general plan of construction of the thallus is similar in *Arthrocladia* ((7) p. 224, (28)) and *Desmarestia* ((13), (22), (25) p. 142, (35)). Transverse (fig. 61 D, E) or longitudinal (fig. 61 B, C) sections through any part of the plant show an axial series of large and much elongated cells (*a*) which, in the older regions of a *Desmarestia*, have thick walls. In the mature parts these axial cells are surrounded by a broad cortical envelope (*co*) exhibiting differentiation into a few layers of small peripheral cells (*p*), packed with lenticular chromatophores (fig. 62 A, *c*), and a wider inner region; its large cells (fig. 61 B, D, *co*) contain few or no chromatophores and are elongate with blunt, tapering ends. Interspersed in the cortex of *Desmarestia* are more or less numerous smaller cells (fig. 61 D, *hy*), which belong to hyphae produced from the inner cortical elements (fig. 61 J, *hy*), while the cells of the axial cylinder sooner or later become enveloped by a special internal system (fig. 61 B, D, *as*) composed of several layers of

[1] This cannot be deemed a sufficient reason for placing them in a separate genus ((29) p. 215).

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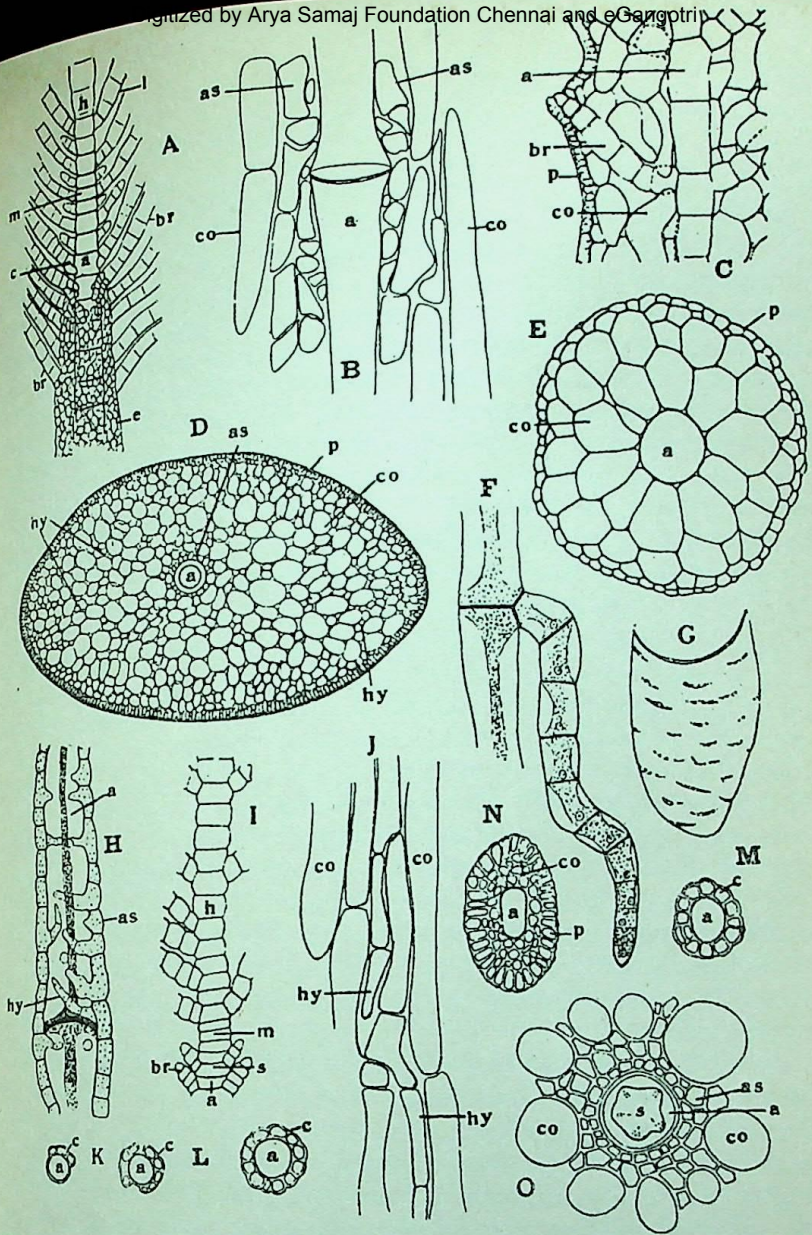

Fig. 61. Structure of Desmarestiales. A, B, D, F–H, J–O, *Desmarestia aculeata* (L.) Lamour.; A, apex of a growing thallus; B, longitudinal section of mature region showing axial cells and internal tissue; D, transverse section of mature thallus; F, formation of downgrowing branch from axial cell; G, part of wall of axial cell with pits; H, development of hyphae from cells of internal system; J, development of hyphae; K–N, transverse sections at successive levels behind the meristem to show development of the cortex; O, axial cell in transverse section, with surrounding tissue. C, I, *D. ligulata* Lamour.; C, part of longitudinal section of young lateral branch; I, apex of a growing branch. E, *Arthrocladia villosa* (Huds.) Duby, transverse section of older part. *a*, axial cell; *as*, internal system; *br*, branch; *c*, primary cells of cortex; *co*, cortex; *e*, envelope of cortical cells; *h*, hair-like tip of thallus; *hy*, hyphae; *l*, lateral; *m*, meristem; *p*, superficial layer of thallus; *s*, cross-wall of axial cell with pits. (A, D after Reinke; B, J after Söderström; C, I after Pease; E after Sauvageau; the rest after Jönsson.)

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small cells with chromatophores. *Arthrocladia* lacks these complications.

The origin of the mature structure can be traced in the brush-like tufts (fig. 60 A) crowning the tips of the diverse branches in young growing plants. Essentially the same features are shown by the numerous laterals of limited growth referred to above; these are far more conspicuous in *D. aculeata* than in *D. ligulata* ((22) p. 332). The cells composing these tufts are densely filled with chromatophores, and they no doubt constitute an important photosynthetic system in the growing thallus. Examination of one of the terminal tufts (fig. 61 A, I) shows that, towards the base of the evident axial row (*a*), there is an intercalary meristem (*m*) composed of flat cells and cutting off elements both above and below. The former replenish the terminal hair (*h*), the uppermost cells of which are constantly wearing away, and each of these segments usually bears one or two unbranched laterals (*l*), which lengthen with the help of a basal meristem.

The numerous segments cut off below the meristem grow out at their upper ends into uniseriate laterals (fig. 61 A, I, *br*) which are paired in *Desmarestia* and formed in whorls of four in *Arthrocladia*; at first these lengthen by means of a basal meristem. These primary laterals later produce delicate branches in opposite pairs (sometimes whorled in *Arthrocladia* (28) p. 98) and thus arise the numerous short pinnate tufts that are arranged along the sides of the long axes (fig. 60 E, *l*). Subsequently the segments bearing the primary laterals exhibit further transverse divisions (fig. 61 I)—mostly two in *Desmarestia*—so that in the older parts only every fourth cell of the series usually bears laterals ((22) p. 334, (35) p. 7); since the axial cells gradually undergo marked elongation, the laterals ultimately become widely spaced.

From the basal cells of the primary laterals, just below the intercalary meristem, the first constituents of the cortical envelope are formed. According to recent accounts ((13) p. 9, (22) pp. 328, 335)[1] the basal cells cut off successively a number of small elements (fig. 61 A, *c*), which multiply by anticlinal division and gradually form a complete one-layered envelope around the elongating axial cell below the lateral (fig. 61 K, L). The cells of this envelope soon undergo periclinal division (fig. 61 M) and, in the further course of events, the outer layer thus produced (fig. 61 N, *p*) behaves as a meristem ((13) p. 9, (28) p. 98) cutting off on its inner side successive elements which enlarge and lengthen to form the cortex enveloping the axial cells. As a result the basal parts of the laterals are gradually buried (fig. 61 A, C).

[1] Reinke ((25) p. 140; cf. also (11) p. 107, (35) p. 8) describes this envelope as being produced from downgrowing and branching threads emerging from the basal cells of the laterals, and a similar origin is recorded for that of *Arthrocladia* ((7), (28) p. 98); later workers on *D. aculeata* and other species have not recognised definite threads.

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According to Jonsson ((13) p. 10) the cells cut off from the superficial meristematic layer enlarge, but show no further division, the meristem accommodating itself by frequent anticlinal division to the progressive widening and elongation of the axis. Its cells at first exhibit a palisade-like shape (fig. 61 N, *p*) and, both in this respect and in the faculty of adding new elements to the internal tissue, this layer resembles the meristoderm of Laminariales (p. 226). In older parts of the thalli the small-celled surface-layers (fig. 61 D, E, *p*) constitute the main photosynthetic system and contrast sharply with the large and often nearly colourless cells of the cortex. It is not clear how long the meristoderm remains active or whether, as seems probable, it divides afresh in each season in the older perennial parts of *D. aculeata*.

As the cortical envelope arises, the meristems of the primary laterals take up a position above their base and commence to divide like that at the tip of the main axis; the lower (inner) segments lengthen and divide in the same measure as the lateral becomes buried, so that its meristem remains at the edge of the expanding axis. Such growth of the laterals is specially marked in the ligulate (leafy) species of *Desmarestia*, where the superficial meristoderm undergoes very plentiful anticlinal division so that the cortical envelope rapidly broadens out to form a flat expanse.

In *Desmarestia* the primary growth above described is succeeded by considerable secondary activity. The cells of the inner cortex grow out into narrow, septate, branching hyphae which push their way between the elements of the cortex and grow mainly in the downward direction (fig. 61 J, *hy*); at first their cells contain chromatophores. These hyphae constitute the small elements (fig. 61 D, *hy*) seen interspersed between the larger ones in transverse sections. They are abundant in the older thalli and are specially numerous in the midribs of the ligulate species; in *D. aculeata* they increase in number with each season ((13) p. 12). Those in the basal parts have thick walls and, as a result of extensive branching, form the bulk of the tissue ((35) p. 14). These structures no doubt fulfil a mechanical function and in this connection it may be noted that the breaking strain of *D. aculeata* may amount to 12 lb. ((4) p. 37).

In the interior of the attaching discs hyphae vastly exceed in number the few primary cells. The upper surface of these discs is, however, composed of vertical rows of rectangular cells ((22) p. 339, (35)), which show a sharp demarcation between the growth of successive seasons owing to the greater length of the cells formed in the early part of each year ((13) p. 37, (22) p. 340).

A further secondary development, that sets in at an early stage, leads to the formation of an internal system of cells with chromatophores (fig. 61 D, *as*). This originates ((13) p. 13) from richly branched hyphae produced from the cortical cells, immediately surrounding the axial thread. The structures in question grow both in the upward and downward directions (fig. 61 B, *as*) and become compacted to form a 3–4-layered envelope of small cells (fig. 61 O, *as*) with abundant chromato-

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phores which directly invests the axial cylinder. It has been suggested (38) that this utilises the carbon dioxide of respiration which is unable to diffuse into the surrounding water (cf. however (3) p. 146). Occasional larger elements surrounded by a similar envelope of small cells with chromatophores may be observed in the inner cortex of older parts. The large elements in question arise as downgrowing branches ((13) p. 26) of the axial cells or of their primary laterals (fig. 61 F). According to Pease ((22) p. 338) such structures are abundantly developed in the ligulate species of *Desmarestia*, where they constitute a branching system of large-celled threads connected directly or indirectly with those of the axial row. They may also occur amid the hyphae of the attaching disc ((13) p. 27, (22) p. 339). In *D. aculeata* Jönsson ((13) p. 14) describes a further system of cells with chromatophores, produced by outgrowth of those surrounding the axial elements and constituting a weft of hypha-like threads within the walls of the latter (fig. 61 H, *hy*; cf. *Spermatochnus*, p. 93).

The elongate axial cells traversing all parts of the thalli are thus provided with more or less numerous branches, and the whole probably constitutes a conducting system ((13) p. 28). The horizontal septa of the component elements show fine pits, which are at first irregularly scattered, although later aggregated into groups, usually of 4 or 5 (fig. 61 O, *s*); there is some evidence that these pits are traversed by cytoplasmic threads ((13) p. 34, (22) p. 339). Jönsson ((13) p. 31) also records pits in the transverse septa of the hyphae and, on the walls between the axial cells and the enveloping secondary system, numerous semilunar areas provided with a fine pitting (fig. 61 G).

The growth of a main axis of a *Desmarestia*-thallus[1] therefore involves (i) the production from the intercalary meristem of new axial segments bearing laterals (fig. 61 A, I); (ii) the formation of the cortical envelope and its gradual increase in thickness by division of the surface-layer (fig. 61 A, K-N); and (iii) the secondary activity due to the production of hyphae from the cortical cells (fig. 61 J) and of downgrowing branches from the main axial series (fig. 61 F). In *Arthrocladia* only the first two stages of this growth are seen. Only a small proportion of the primary laterals develop into branches of unlimited growth. The majority cease to grow when they have reached a certain length, and at the end of the active season both the lateral and its meristem are shed; according to Pease ((22) p. 333) such abscission takes place at a definite predetermined point. Simultaneously the cessation of meristematic activity in the long axes is marked by the shedding of the terminal tuft. In the ligulate forms the basal parts of the branches are entirely buried in the flat expanse of cortical tissue (fig. 61 C, *br*), within which they sometimes appear as lateral veins, while in *D. aculeata* they persist for a time as the thorn-like outgrowths (fig. 60 F), which are a familiar feature of this

[1] The general structure and mode of growth of *Phaeurus* does not differ appreciably from that of a *Desmarestia*.

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species when active growth is not taking place. In *Arthrocladia* Sauvageau ((28) p. 99) also records the origin of laterals of limited growth from the superficial layer of the cortical envelope.

In *Desmarestia aculeata* the new growth in spring originates from the axils of the laterals of previous seasons (fig. 60 B, *n*), or more rarely from the axils of some of the thorns ((21) p. 386, (35) p. 7). At these points there are groups of cells derived from the axial series and forming small swellings; according to Jönsson ((13) p. 6) such rudiments may remain dormant for one or more seasons or be permanently arrested. They give rise to two shoots, only one of which usually develops into a long branch ((35) p. 7); this may grow to a length of upwards of 30 cm. in a single season.

THE REPRODUCTIVE PROCESSES

The sporangia of *Desmarestia*, formed by tangential division of a surface-cell (fig. 62 A, *u*), lie embedded in small groups in the superficial layer of the cortical envelope ((12) p. 142, (15) p. 247, (27), (36)). In *D. aculeata* they are produced in winter after the tufts have been shed ((16) p. 444). The sporangia are of small size and give rise only to a few zoospores; Abe (1) records reduction in the first divisions in *D. viridis*. The zoospores of *D. aculeata* ((30) p. 562; fig. 62 E) possess a single chromatophore (*c*) with the usual apposed eye-spot (*s*); it has not been possible to trace the origin of the long flagellum to this point.

In *Arthrocladia* (fig. 62 B, F, *u*) the sporangia form moniliform chains on the adaxial side of the branches of the first or second order of the whorled laterals of limited growth ((6), (12) p. 139, (18) p. 22, (28) p. 99, (37) p. 336); each sporangium produces about 16 swarmers. Dehiscence by a lateral pore (fig. 62 F) is practically simultaneous in all the sporangia of a chain. Even young plants of *Arthrocladia* may already bear sporangia.

The zoospores of *Desmarestia* (1, 30) germinate according to the usual pattern (fig. 62 C, H). The two types of prothalli become distinguishable at an early stage, since the female (fig. 62 J) have larger cells than the male (fig. 62 K). The tubular oogonia (fig. 62 J, *g*) dehisce apically to liberate the single female cell (*o*) which, as in Laminariales, usually remains adhering to the gelatinised aperture. The male gametophytes (fig. 62 K) are generally more richly branched and comprise more numerous cells which contain fewer chromatophores. The numerous oblong antheridia (*a*) occur singly or in small groups at the ends of the branches, their highly refractive contents including only a single pale chromatophore. The solitary spermatozoid is liberated through a narrow apical aperture (fig. 62 L). Actual fertilisation has not been observed.

Abe ((1) p. 478) describes and figures fusion of swarmers from unilocular sporangia of the same individual; the germlings of these zygotes

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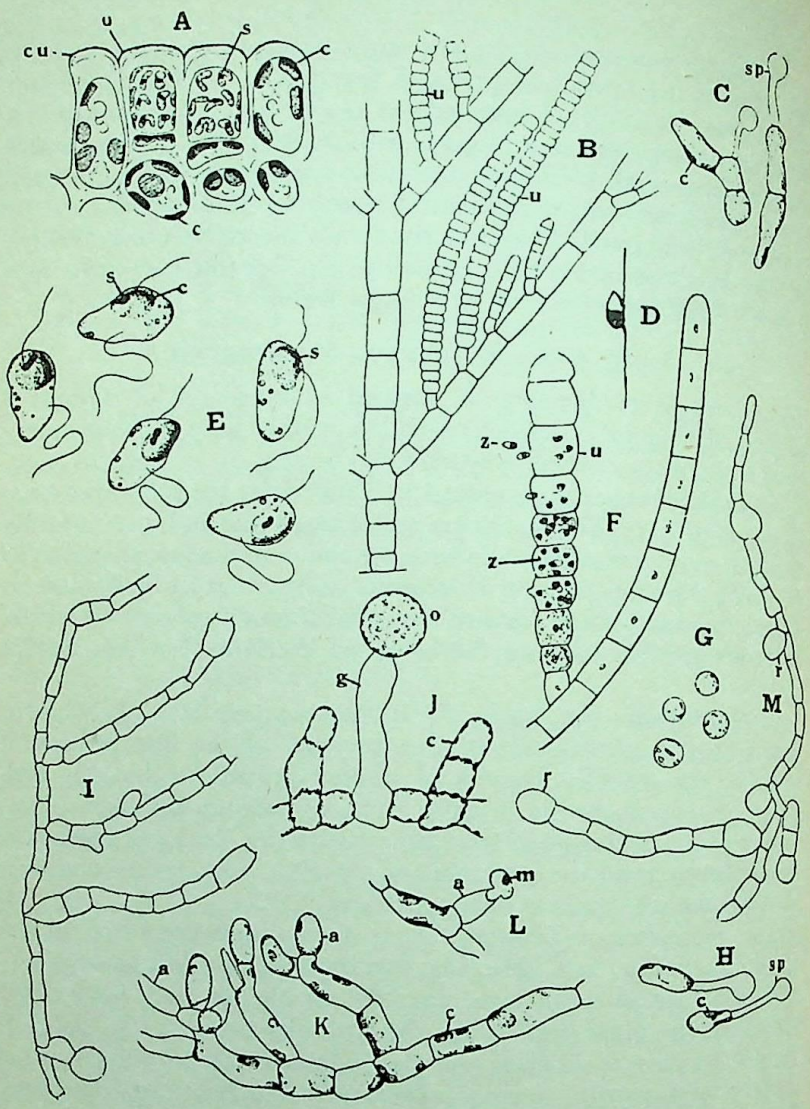

Fig. 62. Reproduction of Desmarestiales. A, C, E, G, H, J–L, *Desmarestia aculeata* (L.) Lamour.; A, section through part of a sorus; C, H, two stages in germination of spores; E, zoospores; G, the same after coming to rest; J, part of a female gametophyte, with dehisced oogonium; K, male gametophyte; L, part of same, liberation of spermatozoid. B, D, F, I, M, *Arthrocladia villosa* (Huds.) Duby; B, part of lateral showing the chains of sporangia; D, zoospore; F, liberation of swarmers from sporangia; I, M, gametophytes. *a*, antheridium; *c*, chromatophore; *cu*, cuticle; *g*, oogonium; *m*, spermatozoid; *o*, ovum; *r*, cells of uncertain function; *s*, stigma; *sp*, spore; *u*, unilocular sporangium; *z*, zoospore. (A after Kuckuck; B, I, M after Sauvageau; D, F after Johnson; the rest after Schreiber.)

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resemble those formed from the zoospores, although they remain sterile.

The zoospores of *Arthrocladia* give rise to extensively branched heterotrichous growths (fig. 62 I, M) which appear to be all of one kind ((28) p. 105). The erect threads bear at their tips and along their sides large rounded cells (*r*) of uncertain function. In Sauvageau's cultures young sporophytes arose from the terminal cells of ordinary branches and he interpreted them as oogonia developing apogamously. He also recognised doubtful antheridia ((28) p. 112), exhibiting occasional dehiscence, borne at the summit of narrower branches of the same prothalli. Germination-stages found entangled amid the latter suggest by their dimensions an origin from the escaped contents of the putative antheridia; the further fate of these germlings was not ascertained. It may be doubted whether these prothalli were normal.

DEVELOPMENT OF THE SPOROPHYTE

The zygotes of *Desmarestia* undergo successive transverse division (fig. 63 B, C) to form an unbranched erect thread (*e*). If the zygote becomes detached from the oogonium before germination, which is likely to be the rule in nature, the formation of branched rhizoids (*r*) sets in at an early stage. In the older embryos (fig. 63 F) plentiful and mainly opposite branching of the uniseriate primary axis takes place. Schreiber ((30) p. 574) draws attention to the similarity between such stages and one of the lateral hair-tufts on the adult thallus.

When the embryo is 3 to 4 weeks old, corticating threads grow out from the lower cells of the main axis (fig. 63 D, E, *c*) in close apposition to the cells below. As they undergo septation and develop branches, the lower part of the axis becomes covered by a continuous cortical investment (fig. 63 A, *co*). At the base of the embryo the threads diverge to form a group of rhizoids (*r*), but farther up their cells divide to form a several-layered cortex. At this stage the axis of the embryo develops, a little way below its apex, a definite intercalary meristem (*m*). The early development of *Arthrocladia* is unknown.

THE STATUS AND AFFINITIES OF THE DESMARESTIALES

The general structure and mode of growth of the sporophytes of *Arthrocladia* and *Desmarestia* present so many points of similarity that, despite the difference in the mode of arrangement of the sporangia, a real affinity is evident. It is therefore hardly justifiable to refer *Arthrocladia* to a separate order ((28) p. 117), although its inclusion in a distinct family, as suggested by Kylin ((17) p. 93), is plausible on the basis of our present knowledge. Much will depend on the nature of the sexual generation of *Arthrocladia*. In its sporophyte it is clearly less specialised than *Desmarestia*.

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The marked degree of correspondence between the prothalli of *Desmarestia* and those of Laminariales induced Schreiber ((30) p. 579) actually to include the Desmarestiaceae in the latter order. This is, however, altogether unwarranted, in view of the fundamental differences between the structure of the sporophyte in the two orders. The Desmarestiales are essentially uniaxial forms acquiring a pseudo-

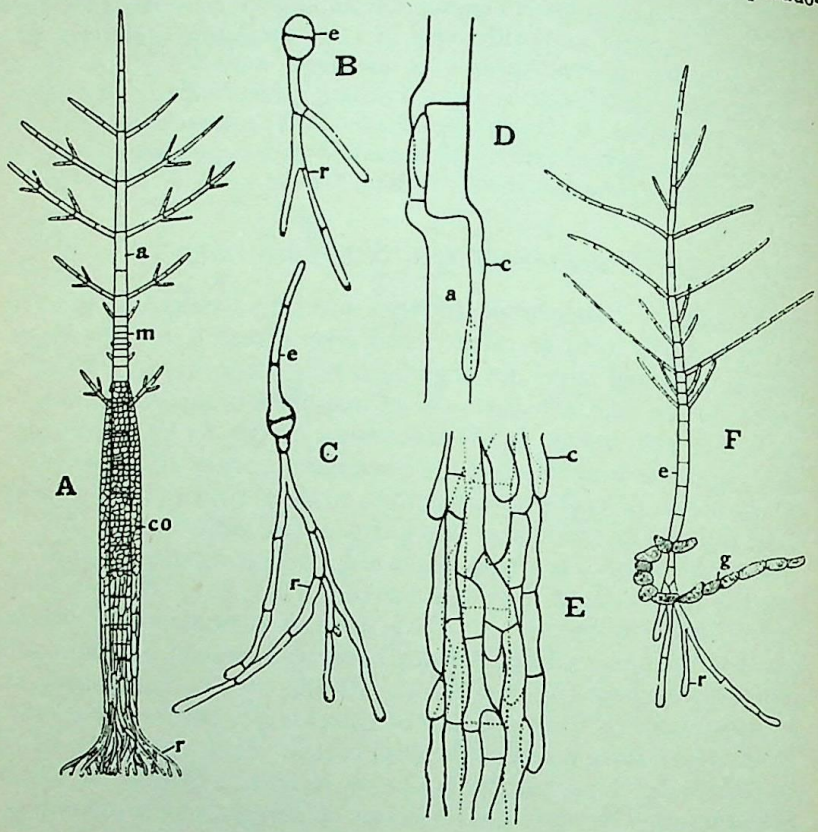

Fig. 63. Early development of *Desmarestia aculeata* (L.) Lamour. (after Schreiber). A, diagrammatic representation of the young plant; B, C, young embryos; D, E, development of cortex; F, older embryo. *a*, axial cell; *c*, cortical threads; *co*, cortex; *e*, erect axis; *g*, gametophyte; *m*, meristem; *r*, rhizoid.

parenchymatous construction secondarily as a result of the development of a cortical investment. This cortical envelope is fundamentally homologous with the corticating threads of a *Spermatochnus* (p. 90) or *Sphacelaria* (p. 268). In the Laminariales, on the other hand, the parenchymatous construction results from the segmentation of a primary filament; in other words the members of this order are highly specialised polystichous types. The Desmarestiales must have their origin among uniaxial forms such as occur in diverse Ectocarpales.

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Despite the different mode of growth, there are considerable analogies between the structure of a *Spermatochnus* and a *Desmarestia*, as Jönsson (13) has particularly emphasised. The resemblances to Sporochnales are discussed on p. 179.

Like other specialised forms the Desmarestiales have lost all traces of heterotrichy in the sporophyte, the growth of the embryo being erect from the first. This, as well as the high degree of elaboration in vegetative structure and the specialisation of the gametophytes, justifies their being grouped in a separate order.

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Order VI. *LAMINARIALES*

The sporophytes of Laminariales include some of the largest forms known among Algae, while they surpass all other Phaeophyceae in morphological complexity and anatomical specialisation. The gametophytes, by contrast, are minute filamentous growths, bearing either oogonia or antheridia (fig. 90). The sporophyte is usually differentiated into a cylindrical stalk or *stipe* and one or many blades or *laminae*. The main region of cell-division lies in the transition zone between stipe and lamina, and this intercalary growth constitutes an important

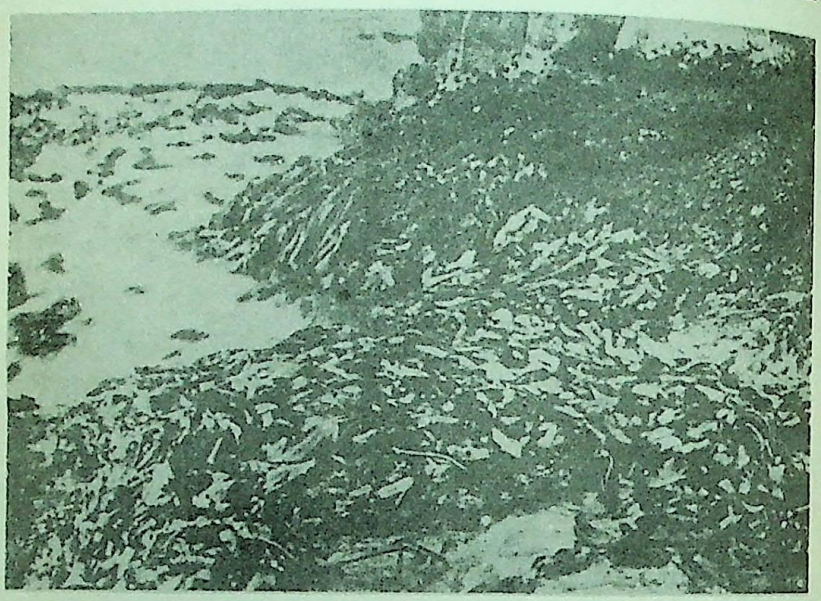

Fig. 64. *Laminaria digitata* (L.) Lamour., exposed at low tide on the coasts of the Faeroes (photo: F. Boergesen). On the left *L. Cloustoni* Edmonds. appears above the surface of the sea. On the rocks on the right are *Rhodymenia* and *Gigartina*.

distinction from Fucales. More significant differences are, however, to be found in the processes of reproduction and in the nature of the life-cycle. The sporangia of Laminariales usually form extensive sori on the blades.

The members of this order are for the most part lithophytes attached to rocks by elaborate holdfasts (fig. 65 N), although they are sometimes epiphytes or found on movable substrata (cf. (156) p. 10, (173) p. 135).[1] They usually occur in the sublittoral region (fig. 64) and

[1] *Laminarias* growing on rock fragments, which are not strong enough to anchor the adult thallus, occasionally get carried out to sea together with their substratum. This sometimes occurs on a considerable scale ((21) p. 36, (183)); plants of *Laminaria Cloustoni* and *Saccorhiza* sometimes bring ashore blocks of rock weighing several pounds.

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not uncommonly form a dense belt not far below low-tide limit where the greater part of the thallus is deeply submerged; they sometimes constitute natural breakwaters. On North European shores they generally follow immediately below the characteristic Fucaceous girdle of the littoral region. Many of the larger Pacific forms, such as *Macrocystis* and *Nereocystis*, are anchored in relatively deep water, the fronds alone floating at the surface (fig. 75 A) by virtue of the great elongation of the stipes and the presence of air-bladders at the bases of the blades. The geographical distribution is dealt with on p. 253.

THE MORPHOLOGICAL FEATURES OF THE SPOROPHYTE

The Family Chordaceae

Chorda filum ((64) pl. 107, (133) p. 35), an annual seaweed of gregarious growth widely distributed in the Northern Hemisphere, though sometimes found between tide-marks, is commoner in the sublittoral region. The hollow, whip-like, unbranched thalli (fig. 81 A) reach a length of 8 metres, although rarely more than $\frac{1}{2}$ cm. in width. Attachment is effected by a small discoid holdfast (*d*) and several thalli sometimes arise from the same base. In quiet localities the plants may form extensive submarine meadows, the upper flagelliform portion floating on the surface. Spiral inrolling is not uncommon. In summer the thalli are often covered with hyaline hairs. *C. tomentosa* Lyngb., sometimes regarded as a variety of *C. filum*, is a smaller and rarer form, covered with an abundance of gelatinous hairs containing chromatophores.

According to Kylin ((93) p. 27) *C. filum* continues to lengthen throughout the summer with the help of a meristematic zone situated a short distance below the apex. Sporangia, which differentiate progressively from below upwards, cover a large part of the surface of the plant. The simple form of the thallus and the relatively unspecialised internal structure (cf. p. 223) justify the reference of *Chorda* to a family of its own.

The Family Laminariaceae

One of the simplest representatives of the true Laminariales is constituted by *Laminaria saccharina* ((64) pl. 289), a widely distributed northern perennial, usually occurring at and to some slight depth below low-tide level. It favours quieter water ((129) p. 180). The smooth round stipe, which is sometimes as thick as a finger and upwards of a metre in length, terminates below in the richly branched holdfast characteristic of Laminariales generally (cf. fig. 65 N), while above it expands into a flat, rather leathery lamina, reaching a length

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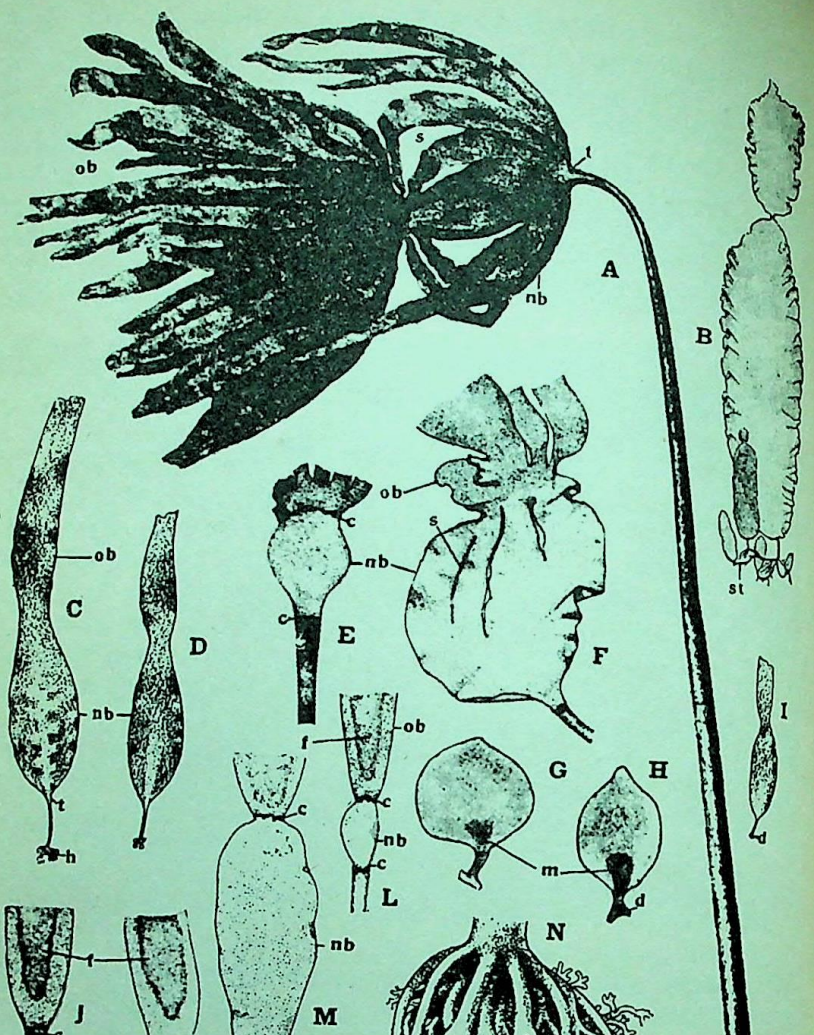

Fig. 65. *Laminaria*. A, *L. Cloustoni* Edmonds., habit. B, *L. Rodriguezii* Born., plant with stolons. C, D, I, *L. saccharina* (L.) Lamour., plants of various ages showing blade-renewal. E, F, *L. Andersonii* Farlow, two stages in formation of new blade. G, H, N, *L. digitata* (L.) Lamour.; G, H, two young plants; N, attaching organ of mature plant. J–M, *L. Sinclairii* (Harv.) Farlow, successive stages in development of new blade. *c*, collar of split tissue at point of blade-renewal; *d*, attaching disc; *f*, sorus; *h*, haptera; *m*, developing medulla; *nb*, new and *ob*, old blade; *s*, slit; *st*, stolon; *t*, transition zone. (A after Foslie; B after Bornet; E, F, J, K, L after Setchell; G, H after Killian; the rest after Sauvageau.)

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of 2 metres; old blades commonly show rows of alternate elevations and depressions within the ruffled margin (cf. fig. 65 C).

As in all Laminariales, the principal formative region is situated in the transition zone between stipe and lamina (fig. 65 C, *t*). By its agency stalk and blade gradually increase in length during the growing season, while in the early months of the year (fig. 65 C, D)[1] a new blade (*nb*) is formed to replace that of the previous season (*ob*). The new lamina (*nb*) first appears at the top of the stipe as a slight widening separated by a marked constriction from that of the preceding year (*ob*), which by this time is usually much frayed and in course of destruction. As the new lamina enlarges, the old one becomes a mere appendage at its apex and ultimately breaks off completely (cf. also p. 241). The unilocular sporangia appear towards the end of the season of active growth and constitute dark brown, irregularly circumscribed sori on both surfaces of the blade; they are usually produced only in older plants ((134) p. 11).

The embryonic stages (fig. 82 A–D, I, p. 224) are anchored by unicellular rhizoids, but relatively soon radial and tangential divisions in the cells at the bottom of the developing stipe result in the formation of a gradually broadening disc (fig. 65 I, *d*) which is attached by rhizoids emerging from its lower cells ((88) p. 250, (134) p. 10). Already towards the end of the first season, however, a whorl of branched haptera arises from the disc and from the stipe above (fig. 65 C, *h*) and further whorls are formed at successively higher levels on the latter as the plant grows older (fig. 65 N), usually at the time of the annual renewal of the lamina.

Among other species of *Laminaria* with an undivided lamina (*Simplices*), *L. solidungula* J. Ag. is characterised by the persistence of the simple attaching disc throughout life ((1) p. 7). *L. longicruris* de la Pyl. ((2) p. 15, (64) pl. 339, (139) p. 845, (141) p. 52) attains to appreciable dimensions, with a hollow stalk reaching 5 metres and a broad blade 4 metres long and stated to become 1½ metres wide ((189) p. 193). Both species are Arctic forms, occurring also on the Atlantic coast of North America down to Cape Cod. *L. japonica* Aresch. ((117) p. 88), important on the coasts of Japan and Siberia ((43) p. 35), is another large form reaching a total length of 12 metres. The Japanese *L. gyrata* Kjellm. ((85), (117) p. 91) is distinguished by the arrangement of the sori in small marginal, subcircular or transversely extended, groups. In *L. religiosa* Miyabe ((204) p. 711) the thickened middle part of the blade is depressed on one and elevated on the other surface, the former always facing the light; the sori first appear on the shaded side and are often restricted to it. This species therefore affords indications of dorsiventrality.

[1] On the New England coast there appear to be two periods of blade-renewal ((167) p. 118, (189) p. 191). The ruffled blade is fully developed in summer, but is replaced in August by a smooth one which lasts through the winter.

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A number of species (e.g. the Mediterranean *L. Rodriguezii* Bornet (17); fig. 65 B; the Pacific *L. Sinclairii* (Harv.) Farl. (176) p. 598; and the Arctic *L. longipes* Bory (120), (166) p. 591) produce, from the region of the holdfast, horizontal stolons which sooner or later turn up at their tips and develop into new plants.

L. saccharina represents a simple type of thallus which is repeated with but little modification in the early stages of development of all Laminariales. A different habit is, however, exhibited by the mature plants of the two other species of *Laminaria* common on North European shores, viz. *L. digitata* ((64) pl. 223; *L. flexicaulis* Le Jolis (36), (101) p. 91), also found on the Atlantic shores of North America, and *L. Cloustoni* (*L. hyperborea* Foslie (100) p. 533); the latter usually occupies a lower level (fig. 64) than the former ((58) p. 893, (91) p. 100, (183)). In these species (*Digitatae*) the greater part of the blade is divided into numerous segments (fig. 65 A). *L. digitata* has a pliable stipe ((210), p. 325), while that of *L. Cloustoni* is firm and wrinkled, usually bearing numerous epiphytic Florideae. The sori of *L. digitata* form scattered patches on the blades (fig. 88 A), whilst in *L. Cloustoni* they appear as large irregular areas with but little free surface between them ((156) p. 188). The holdfasts ((37) p. 5; fig. 65 N) resemble those of *L. saccharina*.

Young plants of both species have an undivided blade and are indistinguishable from those of *L. saccharina* ((8) p. 15, (100) p. 549, (134) p. 13). A new blade is formed in the same way during the winter and this is at first entire, but, as it enlarges, successive short longitudinal splits[1] arise within the lower portion, the first ones appearing near the outer margin (cf. fig. 65 F, *s*). Gradually the splits extend to the front edge of the new lamina, which consequently gets resolved into separate segments (fig. 65 A, *nb*); the middle ones commonly become completely free only after the old blade has worn away. In subsequent years the new blade (fig. 65 E) likewise originates as a dilatation at the summit of the stipe and becomes segmented in the same way.

In some of the perennial digitate species such blade-renewal probably takes place repeatedly over a period of years, but this seems to vary with the latitude and depends on environmental conditions ((156) p. 134). Certain species are more long-lived than others. Sauvageau ((156) p. 14) concludes that plants of *L. Cloustoni* persist for 10–20 years and Foslie ((37) p. 46) records old specimens with stipes 5 metres long. According to Yendo ((206) p. 56), on the other hand, the *Laminarias* of Japan live for only two years and show only one period of blade-renewal. *L. ephemera* Setchell ((168), (172) p. 92) (*Renfrewia parvula* Griggs (52), (54) p. 51), an annual attached by a simple disc throughout life, exhibits relatively little splitting of the blade.

[1] The mode of origin of the splits in *Laminaria* and other Laminariales is dealt with on p. 240.

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Several monotypic genera which are characteristic of the North Pacific, while retaining the simple habit of a *Laminaria saccharina*, exhibit diverse modifications in their fronds. In *Pleurophycus* ((146) p. 427, (168) p. 123, (176) p. 606), which is probably an annual, the middle of the blade shows a shallow fold simulating a broad midrib and contrasting markedly with the undulate wings. The blade of *Cymathere triplicata* ((1) p. 29, (8) p. 20, (53), (175) p. 264, (176) p. 608; *Laminaria triplicata* Post. & Rupr. (126) pl. 10; fig. 66 A) is provided with three narrow longitudinal folds (*r*) throughout its length; it may be as much as 4 metres long and 22 cm. broad, although the stipe does not usually exceed 5 cm. The sori are restricted to the base of the blade. *Cymathere* is fixed by a discoid holdfast and frequents relatively quiet water.

In *Costaria* ((8) p. 19, (176) p. 609, (204);[1] figs. 66 F; 70 A) the blade is traversed by five prominent longitudinal ribs which project alternately on the two surfaces (cf. fig. 66 I, *r*) so that three are visible on the one and two on the other; on the surface opposite to each rib there is a corresponding depression, while between the ribs there are numerous puckerings (*b*). The blade continues to widen after it has reached its full length and occasional perforations are formed in much the same way as in *Agarum* (cf. below). In the young plant (204) the midrib arises first (fig. 66 C, E, *r*) and then, successively, the lateral ribs (fig. 66 D). The sori occupy the longitudinal depressions, as well as the hollows around the perforations ((76) p. 237).

A greater degree of specialisation is seen in *Agarum* and *Thalassiophyllum*. The former ((2) p. 18, (69), (134) p. 19), represented by several perennial species in Northern Asia and America, has only a short stipe (fig. 66 B). The mature elongate blade is provided with a prominent midrib (*r*) and is pierced by numerous large perforations (*p*) ((8) p. 18, (69)) which are lacking in young plants (fig. 66 G). In *A. cribrosum* (*A. Turneri* Post. & Rupr. (126) pl. 22) the lower margins of the lamina are distinctly inrolled ((170) p. 125; fig. 66 H). Most authorities (see (134) p. 18) state that the blade is renewed periodically as in a *Laminaria*, but according to Humphrey ((69) p. 200) there is continuous growth at the base as the apex wears away (cf. *Alaria*). The sori are formed on either surface of the blade.

Young plants of *Thalassiophyllum* ((170) p. 123) have a very short stipe bearing a broad cordate blade (fig. 67 A), the lower margins of which soon thicken; growth in width of the blade continues for a long time (fig. 67 B, C) so that it soon becomes broadly reniform (fig. 67 D). At an early stage, as a result of unequal surface growth, the lower edges undergo inrolling (*s*) and their thickened margins come to lie in the centre of the developing scrolls (cf. *Agarum cribrosum*). The degree of inrolling increases as the blade widens (fig. 67 E), while simultaneously the median part of the latter (*b*) undergoes progressive erosion.

[1] *Costaria reticulata* Saunders (145) is a member of Lessoniaceae (*Dictyoneuropsis* (215) p. 651).

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This ultimately results (fig. 67 G, H) in the complete separation of the two large scrolls, the basal parts of which have thickened to form two arms diverging from the apex of the original stipe (fig. 67 F, H, *a*).

The keels constituted by the thickened basal margins of the lamina are protected within their appropriate scrolls, but the exposed edges

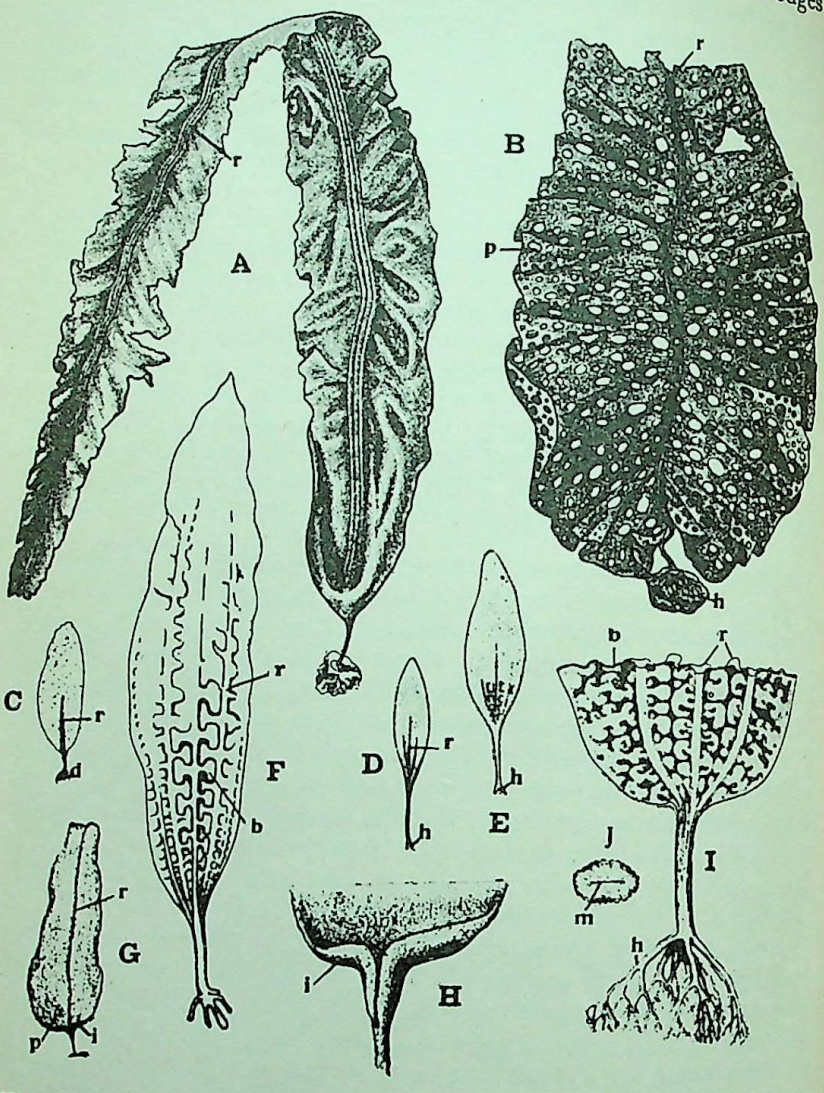

Fig. 66. A, *Cymathere triplicata* (Post. & Rupr.) Ag., habit. B, G, H, *Agarum cribrosum* (Mert.) Bory; B, habit; G, young plant; H, basal part of older blade. C–F, I, J, *Costaria costata* (Turn.) Saund.; C–E, young stages; F, older plant; I, basal part of a mature plant; J, transverse section of stipe. *b*, puckerings of blade; *d*, attaching disc; *h*, hapteron; *i*, infolded margin of blade; *m*, medulla; *p*, perforation; *r*, rib. (A, B after Postels and Ruprecht; G, H after Reinke; the rest after Yendo.)

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of the two secondary blades undergo progressive erosion and so appear more or less ragged (fig. 67 H, *e*). The meristem that brings about the gradual enlargement of each secondary blade lies along the edge of the keel. As the blades spread out, they develop numerous perforations (fig. 67 G, H, *p*) which are arranged in longitudinal series parallel with the keel (fig. 67 I); the edge of the perforations is at first

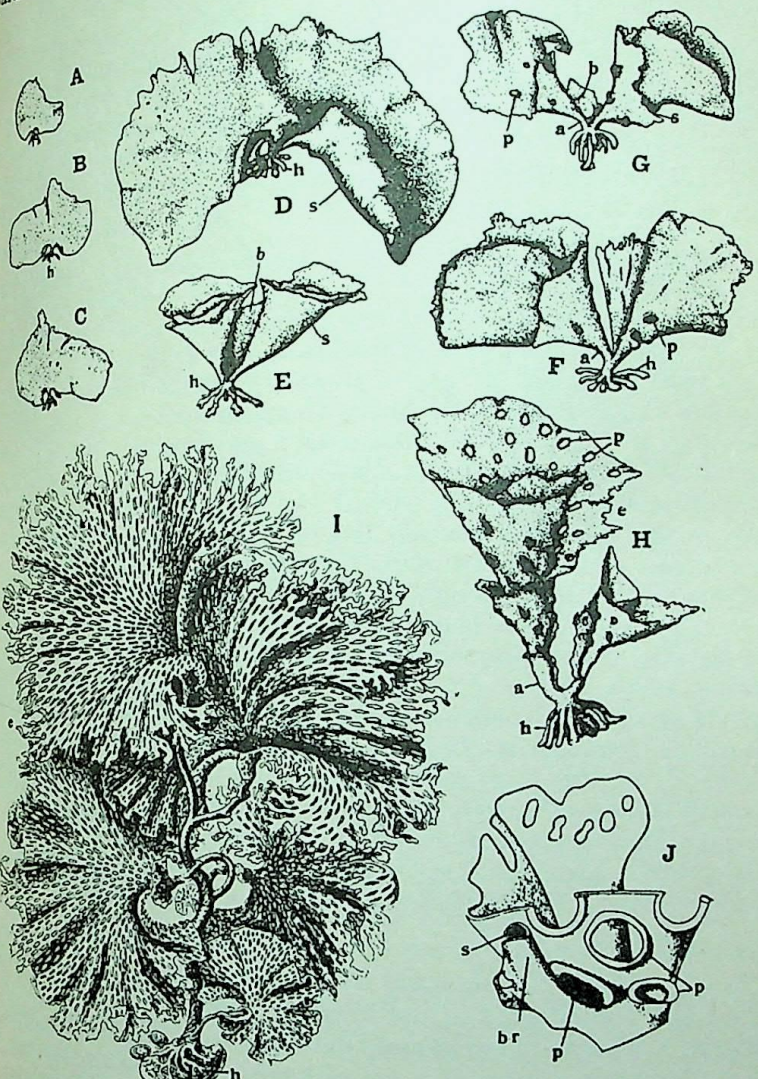

Fig. 67. *Thalassiophyllum clathrus* (Gmel.) Post. & Rupr. A–H, successive development (see text); I, mature plant; J, details of adventitious branch-formation. *a*, the two arms formed from the basal scrolls; *b*, primary blade; *br*, branch; *e*, eroded edge of blade; *h*, hapteron; *p*, perforation; *s*, scroll. (I after Postels and Ruprecht; J after Rosenthal; the rest after Setchell.)

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revolute ((138) p. 137). For a time the two secondary blades develop uniformly (fig. 67 F), but later one usually takes the lead ((176) p. 614) and assumes a more or less erect position. As growth continues its basal portion elongates to form a false stipe (fig. 67 H, *a*), which usually becomes twisted. According to Rosenthal ((138) p. 140) the branches found on mature plants are all adventitious, originating from the lower edge of certain perforations close to the thickened keel (fig. 67 J, *br*). The adult plants ((126) pl. 18, (138) p. 136), which grow in dense thickets just below low-water mark, reach to a height of about a metre. The thick twisted stipes (fig. 67 I) bear numerous branches each terminating in a firm coriaceous blade inrolled at its base and pierced by numerous holes. Anchorage is effected by haptera (*h*) arising from the base of the original stipe. The sori form irregular dark brown areas on the blades.

A less complex form is attained by the allied genus *Hedophyllum* ((54) p. 27, (146) p. 429, (168), (170) p. 119, (205) p. 269), the mature plants of which (fig. 68 A, B) are attached by numerous haptera (*h*) arising from the thickened basal margins of the blade. The young plant (fig. 68 C) has a short flattened stipe and at an early stage the base of the lamina becomes decumbent. In *H. sessile* (*Laminaria sessilis* Ag.; *L. apoda* Harv. (63) p. 167) the older blades split into two or more segments (fig. 68 A). In *H. subsessile* (fig. 68 B), however, the median part of the primary lamina wears away leaving two secondary blades (*sb*) at the ends of the thickened margins (*m*) of the former, which appear as bifurcations of the original stipe (*s*); the basal margins exhibit some inrolling (fig. 68 B), although this is more marked in *H. spirale* Yendo ((120) p. 54, (202)). There is much resemblance to *Thalassiophyllum*, but the inrolling is not pronounced and there are no perforations. *Hedophyllum sessile* ((170) p. 126) appears to constitute a link between the digitate species of *Laminaria* and *H. subsessile* which in its turn, via *H. spirale*, approaches *Thalassiophyllum*. In *Arthrothamnus bifidus* (Gmel.) J. Ag. ((1) p. 25, (9) p. 14, (176) p. 619, (199), (202) p. 168) the primary lamina ultimately disappears completely except for its decumbent basal margins from which the secondary blades arise. The same process is repeated again and again and thus a dichotomising rhizome bearing numerous fronds is gradually produced.

A different structure is seen in *Saccorhiza bulbosa* ((10), (125), (156) p. 32), an annual[1] found on the Atlantic shores of Europe and North Africa and sporadically in the Western Mediterranean ((156) p. 21, (208)); it is not infrequent at and below low-water mark in the British Isles. The mature plant (fig. 69 A) has a digitate blade, sometimes exceeding 2 metres in length ((156) p. 89) and borne at the end of a flattened stalk (*s*) which may be 60 cm. long. The stalk is spirally twisted in its lower portion and below the twist there is a large in-

[1] Spence ((183) p. 284), however, records the persistence of plants into the summer of the second season.

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verted bell-shaped outgrowth (*b*), which may reach 40 cm. in diameter and covers in the basal part of the stalk, as well as the original attaching disc. Numerous haptera (*h*) arise from the margin of the bell, while the outer surface often bears similar unattached structures.

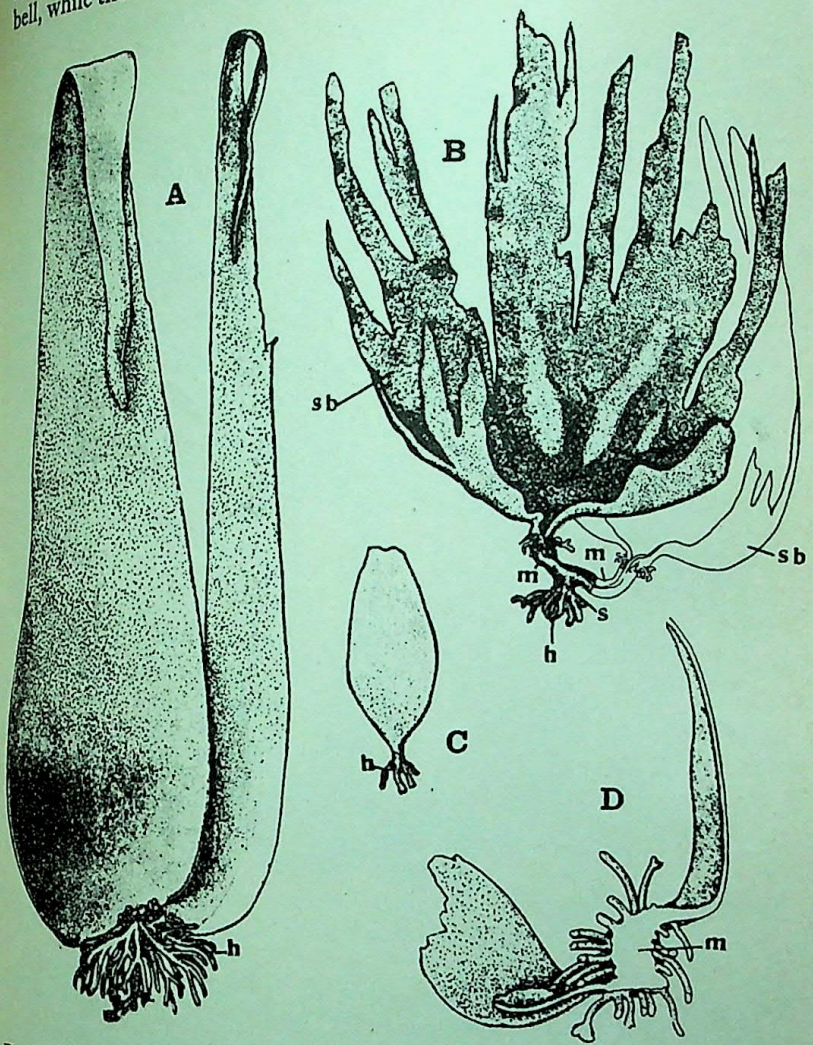

Fig. 68. *Hedophyllum* (after Setchell). A, C, D, *H. sessile* (Ag.) Setch.; A, habit of mature plant; C, young stage; D, later stage showing the decumbent base of the blade. B, *H. subsessile* (Aresch.) Setch., habit. *h*, haptera; *m*, meristem; *s*, stipe; *sb*, secondary blade.

The early stages (190) are of the usual type. The bell develops from the transition zone (fig. 69 B, *b*) and completely covers in the short stipe, while subsequently the same meristem gives rise to the flattened stalk which intervenes between bell and blade. This stalk ultimately develops undulating wings (fig. 69 A, *w*) upon which the

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sori are usually formed, but they can also arise on the blade, as well as on the inner and outer surfaces of the bell (153). The latter survives throughout the winter after the rest of the plant has perished. Gardiner (46) also records formation of sporangia on the haptera.

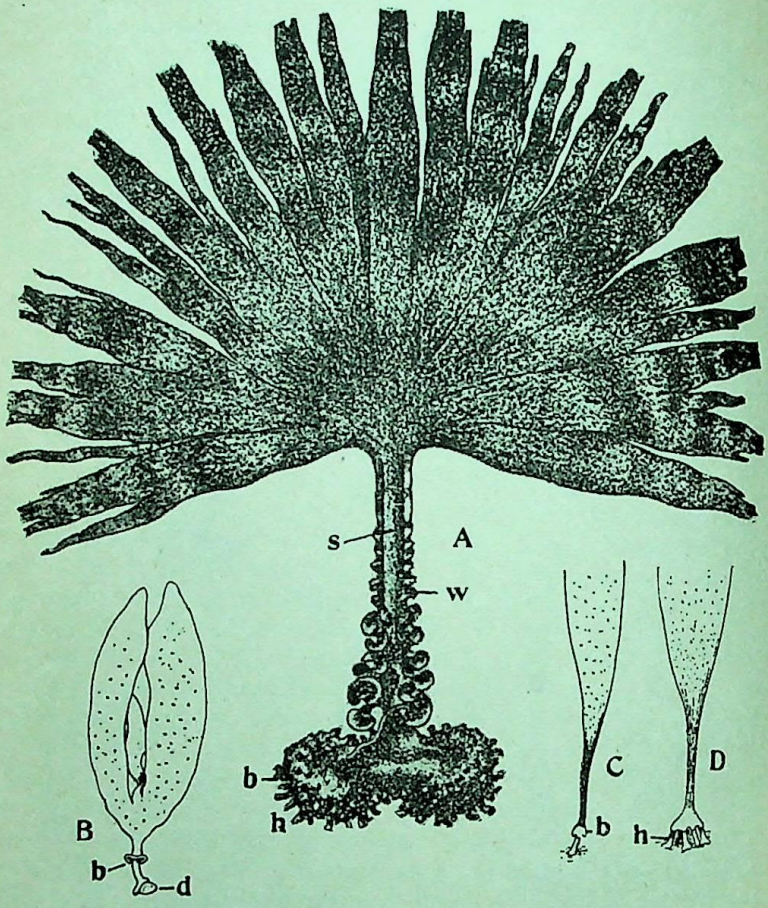

Fig. 69. A, B, *Saccorhiza bulbosa* De la Pyl.; A, small mature and B, young plants. C, D, *S. dermatodea* (De la Pyl.) J. Ag., lower parts of young plants of successive ages. *b*, bell; *d*, attaching disc; *h*, hapteron; *s*, stipe; *w*, wing. (A after Sauvageau; B after Barber; C, D after Setchell.)

Another species, *S. dermatodea* ((38) p. 74, (161)), which is sometimes ((85*a*) p. 254) referred to a separate genus *Phyllaria* owing to the position of the sori at the base of the blade, is widely distributed in the Northern Hemisphere. Here the stalk is simple and the bell (Setchell's rhizogen) is quite a small structure (fig. 69 C, D), although again serving for attachment. *Phyllaria reniformis* (Lamour.) Rostaf. occurs in the Mediterranean and the adjacent parts of the Atlantic.

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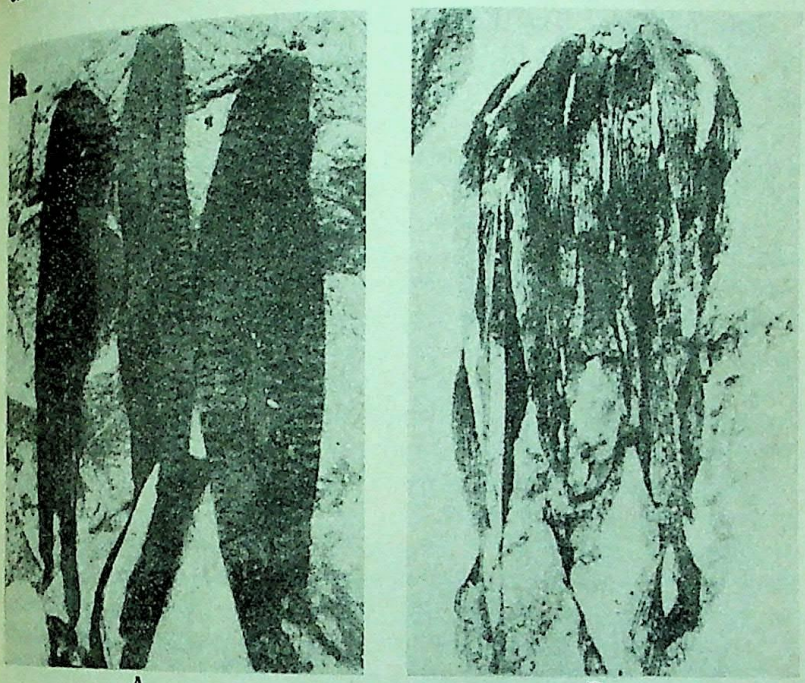
The Family Lessoniaceae

The splitting of the lamina, seen in diverse genera above considered, does not usually extend into the transition zone, so that the meristem remains a single entity; meristematic activity may, however, subsequently concentrate mainly in other regions, as for instance along the edge of the keel in *Thalassiophyllum*. In the forms, which Setchell groups as Lessoniaceae, on the other hand, the process of splitting extends also into the transition zone, so that the secondary blades are



A B

Fig. 70. A, *Costaria costata* (Turn.) Saund. B, *Dictyoneurum californicum* Rupr. (photos: F. E. Fritsch, Monterey Peninsula, California).

each provided with a part of the original meristem and can thus develop secondary stipes of their own. This is one of the characteristic features that underlies the construction of such genera as *Lessonia* and *Macrocystis*.

The first species to be mentioned is *Dictyoneurum californicum* ((144) p. 80, (176) p. 621), which is confined to Pacific North America. The young plant, so far as known, is of the usual pattern. Its short stipe soon becomes prostrate and develops into a flat and rather thin organ attached to the substratum by marginal haptera (fig. 70 B, *s*). The lamina segments by means of successive splits that originate in the transition zone and gradually extend outwards. The short stipes of the secondary blades become decumbent and are attached to the

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substratum in the same way as the primary one and, since this happens time after time, the front part of the attachment system gradually advances, while the older part behind dies away; in this way a single plant gives rise to a clump. Older blades exhibit a network of coarse ribs (fig. 70 B). Broad irregular sori appear each year on both surfaces of the blades. *Dictyoneurum* is distinguished from other Lessoniaceae by the procumbent development of the stipe. In *Dictyoneuropsis* ((215) p. 651) splitting takes place through the broad midrib of the young lamina, the secondary blades regenerating a new half along the exposed edges.

The chief centre of distribution of *Lessonia* ((9) p. 8, (51) p. 641, (96), (179) p. 69, (180) p. 47, (214) p. 57) is in the Southern Hemisphere (see map 2, p. 252). The young stages ((60) p. 457, (179) p. 73) show the usual habit (fig. 71 A), but a median split (fig. 71 B, *s*) soon arises near the base of the blade resulting in two segments (fig. 71 C, F) provided with short pedicels (*p*) which appear as forks of the underlying stipe. The original meristem is thus segregated into two entities (*m*), each contributing not only to the enlargement of the appropriate secondary blade, but also to the lengthening of the pedicel below. The secondary blades split in the same way (fig. 71 C), and this is repeated time and again. Commonly one fork develops more vigorously than the other (fig. 71 E) and, since the pedicels of successive stronger forks become arranged in a straight line, a sympodial axis (*a*) is formed, upon which the weaker ones appear as laterals.

In some species (e.g. *L. laminariaeoides* ((9) p. 10, (126) pl. 38, *e*) the primary stipe remains short, but in others (*L. flavicans*, fig. 71 D; *L. nigrescens*, fig. 71 E) it lengthens progressively to form a main trunk upon which the numerous secondary blades are borne. One of the most striking species is *L. flavicans* (*L. fuscescens* Bory ((126) pl. 3; *L. ovata* Hook. et Harv.), the mature plants of which resemble small trees (fig. 73 D). The thick stipe divides again and again in its upper portion, the ultimate branches ending in long lanceolate blades. Harvey ((60) p. 457) states that the plants may reach a height of 4 metres, while the main stipe may have the thickness of a human thigh. According to Skottsberg ((179) p. 74) the stipe increases in thickness with each division of the lamina. The sori of *Lessonia* are formed on the basal parts of the blades.

Postelsia palmaeformis ((144) p. 75, (176) p. 624, (182)), an annual confined to the Pacific shores of North America, although of appreciably smaller dimensions, resembles the arboreal *Lessonias* in habit. One of the most striking of the Laminariales, it well deserves the popular name of Sea Palm. The thalli (fig. 72) have short thick upright stipes surmounted by a pendent mass of blades. They grow gregariously in habitats exposed to the full violence of the waves, and it is a remarkable sight to see such a forest of *Postelsia* uncovered at low tide and unaffected by the battering of the waves to

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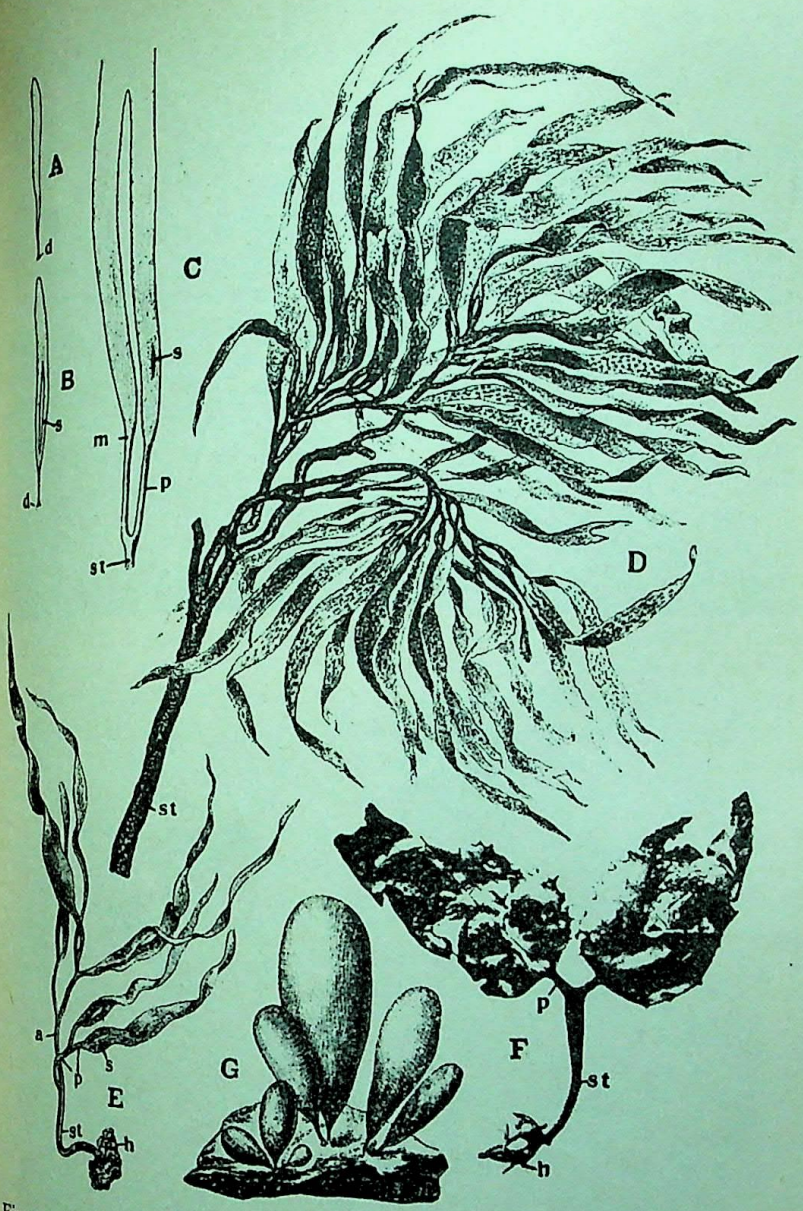

Fig. 71. A–F, *Lessonia*. A–C, E, *L. nigrescens* Bory; A–C, successive stages in development of the blade; E, habit of older plant. D, F, *L. flavicans* Bory; D, single branch of an older plant; F, young plant. G, *Adenocystis utricularis* (Bory) Skottsb., group of plants. *a*, sympodial axis; *d*, attaching disc; *h*, hapteron; *m*, meristem; *p*, stipe of secondary blade; *s*, slit; *st*, stipe. (A–C after Reinke; D, E after Postels & Ruprecht; F after Skottsberg; G after Harvey.)

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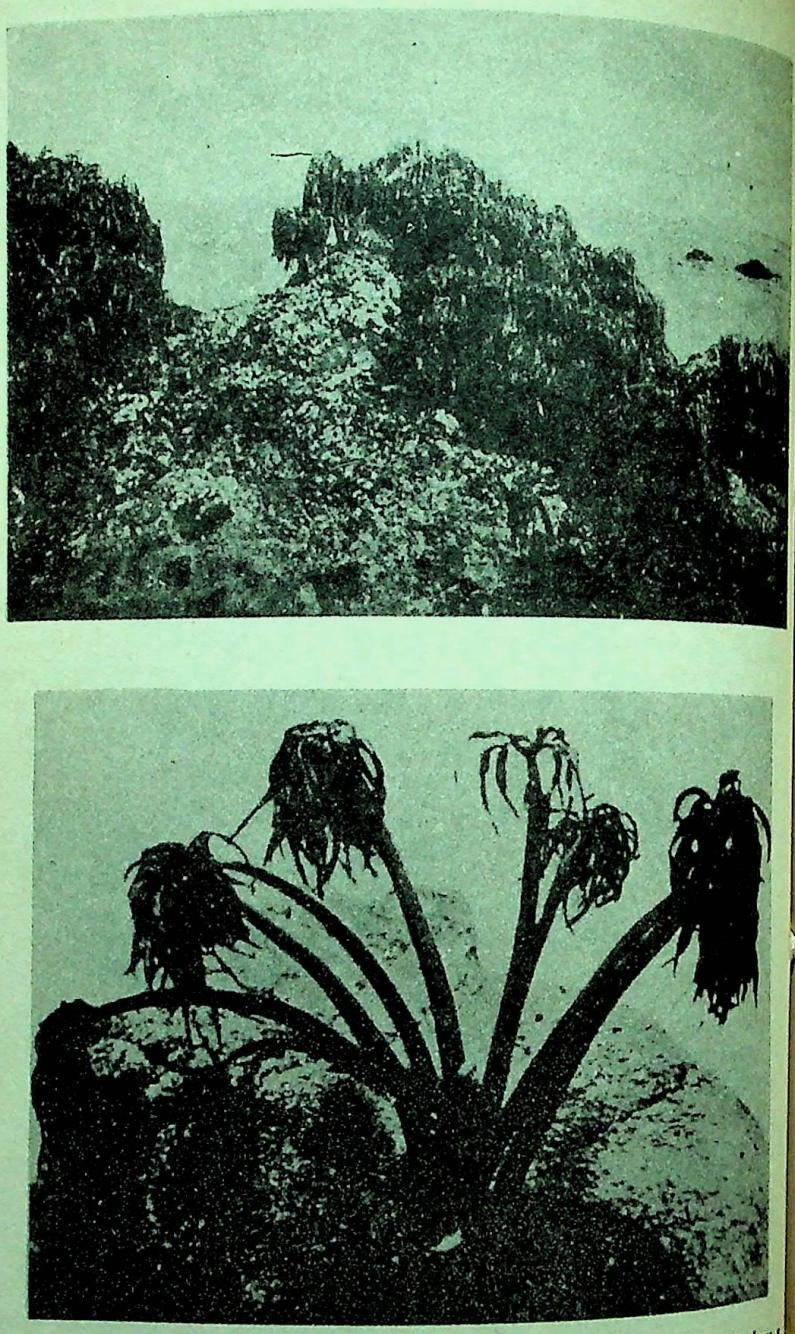

Fig. 72. *Postelsia palmaeformis* Rupr. Above, several dense groups; below, a few plants on a larger scale. (Photos: F. E. Fritsch, Monterey Peninsula, California.)

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which it is subjected. The numerous blades arise by splitting in the transition zone, much as in *Lessonia*. The stipe, from 40 to 60 cm. high, is hollow, but the many short pedicels at its summit are solid. Each bears a falcate blade, traversed on both surfaces by deep longitudinal grooves within which the sori develop.

Nereocystis and *Macrocystis* are distinguished by greater elongation of the stipe and by the huge size attained by the mature thalli. The former ((9) p. 5, (105), (126) p. 8), the Bull Kelp of the Americans, despite its dimensions, is probably in the main an annual seaweed (cf. also (39), (171), p. 129) lasting from February to the following November or December. The young plants (7, 41) are of the usual type (fig. 73 B, E), but soon exhibit rapid lengthening of the stipe, although at first it remains slender and very flexible. Near its summit and beneath the transition zone a spherical air-bladder (*v*) arises at an early stage and, soon after, the blade develops the first split (*s*), which extends down to the bladder and divides the lamina into approximately equal halves. As the bladder enlarges (fig. 73 C), the short stalks (*p*) of the secondary blades become separated. Successive splitting of the blades takes place, as the stipe elongates and the float enlarges, so that the older plant (fig. 73 A) bears numerous lanceolate fronds, not uncommonly grouped in two or more bunches corresponding to the primary divisions of the lamina. The rather thick solid stipes of such plants are anchored by an elaborate holdfast, which is up to 30 cm. in diameter. The sori form elongate areas, reaching a metre in length, on both surfaces of the blades; after liberation of the swarmers the whole fruiting region drops out (59).

Frye (41) states that the second and third splittings of the blade are often unequal, the larger segment being to the outside; he sees in this a resemblance to *Pelagophycus* (p. 211). *Nereocystis* favours habitats where the tide is swift and usually grows in 5–8 fathoms of water ((39), (105), (135) p. 86); the length of the stipe depends on the depth (70). The plants often grow in dense masses (39) and the largest are found in the vicinity of the Arctic. The stipes were formerly employed as fish-lines by the natives, while the huge floats were used to siphon water from the boats ((135) p. 91). According to Macmillan ((105) p. 278) the thallus reaches a length of 100 metres, with air-bladders 2–3 metres long and up to 15 cm. in diameter, while the blades are stated to become 15 metres long; most other authorities give considerably smaller dimensions and it remains doubtful whether the plants are ever more than 50 metres in length (cf. (39), (42), (135) p. 86, (171), (176) p. 624). The mature floats are more or less pear-shaped and separated by a constriction from the stipe below. They rest on the surface of the water, while the numerous blades are slightly submerged. Older stipes bear irregular outgrowths which have been regarded as homologous with the haptera ((105) p. 276).

Macrocystis ((60) p. 461, (138) p. 107, (178), (179) p. 80), the largest of the perennial seaweeds, has its main centre in the Southern Hemi-

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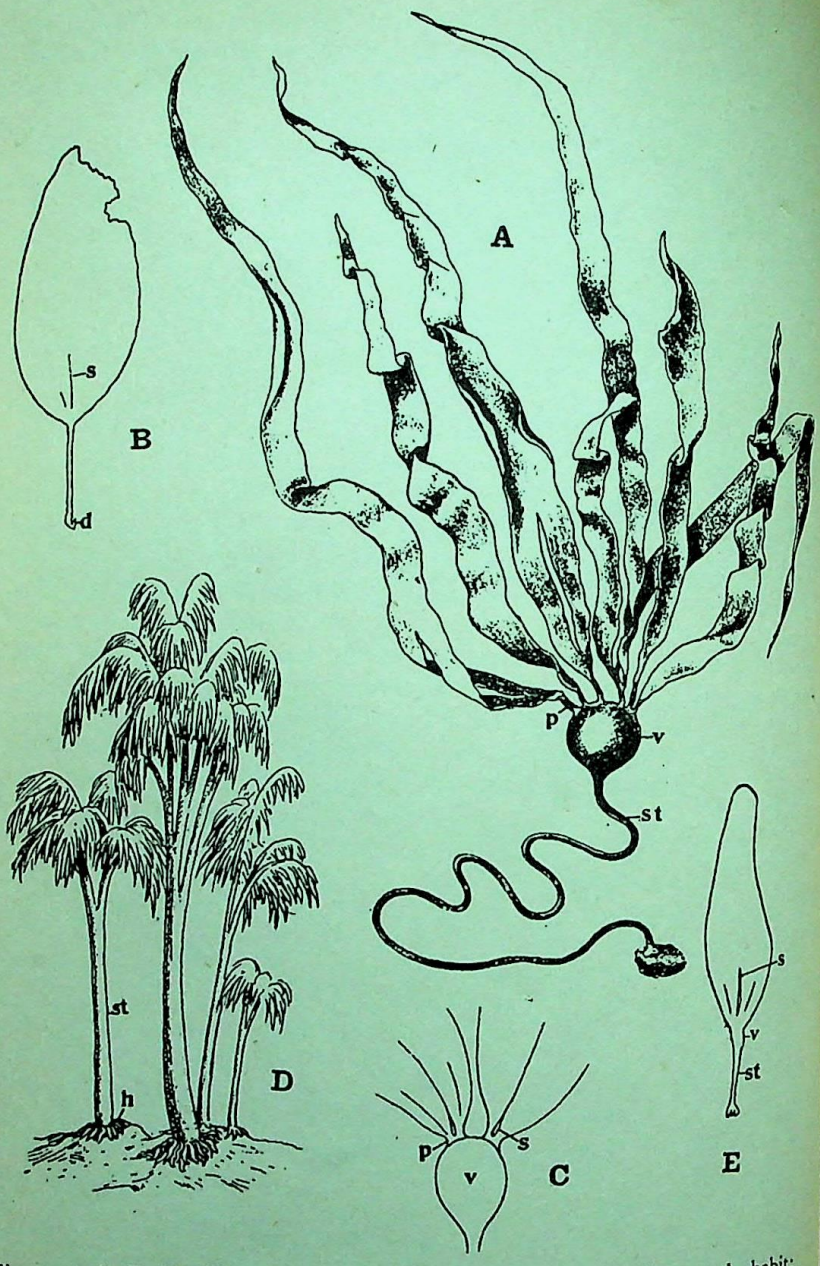

Fig. 73. A–C, E, *Nereocystis Luetkeana* (Mert.) Post. & Rupr.; A, habit; B, E, young plants; C, early splittings of the blade. D, *Lessonia flavicans* Bory, habit. *d*, attaching disc; *h*, hapteron; *p*, pedicel of blade; *s*, slit; *st*, stipe; *v*, air-bladder. (A after Postels & Ruprecht; B, C after Macmillan; D after Hooker and Harvey; E after Hartge.)

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sphere, although also well represented on the western shores of America (see map 2, p. 252). It usually grows in 8–10 fathoms of water. According to recent accounts[1] the thalli of *M. pyrifera* (fig. 74 A) attain a maximum length of 60 metres. Above the holdfast (*h*) there follows a long slender stalk (*st*, a centimetre or less in width), which often bears a number of scattered blades and trails out obliquely to the surface of the water, where the rest of the thallus floats horizontally. This floating portion (fig. 74 C) bears a dense double row of shortly stalked lanceolate blades (*bl*), 1–1½ metres in length; the blades have a corrugate surface and bear short spines along their margins, while at the base of each is a spherical to pyriform air-bladder (*b*). On the older parts the blades usually disintegrate and at most only the air-bladders remain. The holdfast of *M. pyrifera* may be nearly a metre in diameter ((176) p. 627, (179) p. 96) and is of the usual type (fig. 74 A, *h*), but in *M. integrifolia* Bory ((8) p. 22, (68) p. 60, (174) p. 448, (176) p. 628), found on the Pacific coasts of America,[2] attachment is effected by a flattened, prostrate richly branched organ bearing haptera along its margins and dying away behind as it grows on in front (cf. *Dictyoneurum*).

The development of the mature structure from the embryonic stage (fig. 74 F) takes place in essentially the same way as in *Lessonia* ((18) p. 11, (50) p. 323, (72) p. 109, (134) p. 34, (138) p. 107, (174) p. 449, (178), (179) p. 82, (193) p. 802). A median split divides the young blade into two equal halves (fig. 74 G), but before the split has extended to the apex of the lamina further splits (*s2*) are formed on either side. As the tertiary blades become free (fig. 74 B), intensive marginal growth of the original lamina results in a rapid enlargement of the two outer blades (*1*, *1*), while the inner ones (*2*, *2*) remain narrower; according to Skottsberg ((179) p. 85) the next splits always arise in the outer segments (fig. 74 B).[3] Both of the latter (fig. 74 D, E, *b2*) give rise to elongate floating shoots in the way described below, while the inner ones may also develop into such long shoots, although the latter are retarded in growth as compared with the others.[4]

In the subsequent course of events, after each process of splitting,

[1] See (24) p. 168, (42) p. 475, (97) p. 499, (179) p. 103. Larger dimensions are given by earlier authors (cf. (193) p. 806). South African plants are small ((213) p. 21).

[2] It has been suggested that this species, which occurs also in South Africa (29), is but a shallow-water form of *M. pyrifera* ((176) p. 627), but Smith ((215) p. 651) regards it as distinct.

[3] The drawing of Reinke (134), reproduced in fig. 74 G, shows just the opposite. Skottsberg suggests that this specimen, drawn from herbarium material, had undergone displacement of its parts in mounting.

[4] The later-formed haptera commonly take their origin from the branches of the first fork, so that several plants may appear to arise from the same holdfast or may even seem to originate adventitiously from the haptera (193). Skottsberg ((179) p. 96) was, however, unable to find any evidence for such an origin.

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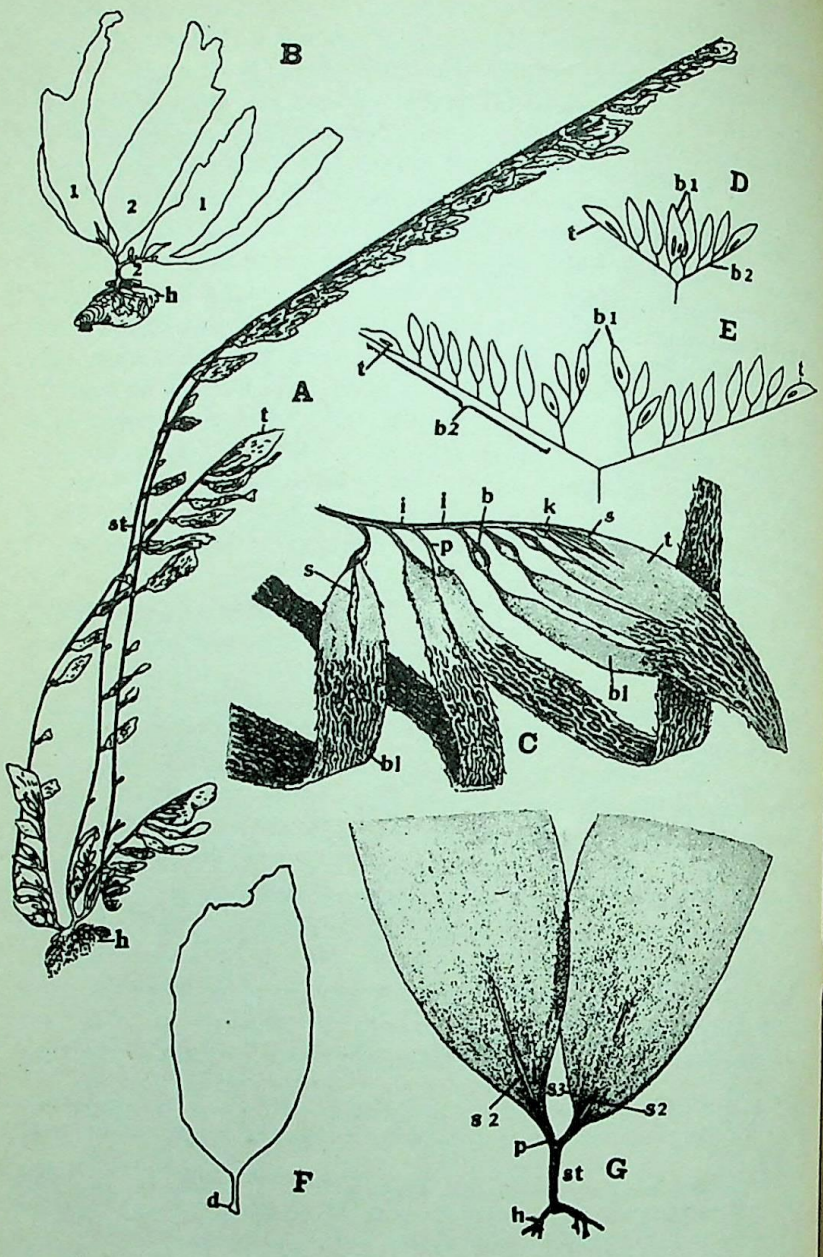

Fig. 74. *Macrocystis pyrifera* (Turn.) Ag. A, diagrammatic representation of an older plant; B, G, early stages of development; C, tip of growing plant; D, E, diagrammatic representation to show mode of development of thallus; F, embryo. *b*, air-bladder; *d*, attaching disc; *b* 1, *b* 2, *bl*, successive blades; *h*, hapteron; *i*, internode; *k*, keel; *p*, pedicel; *s*, *s* 1, *s* 2, *s* 3, slits; *st*, stipe; *t*, terminal blade. (C after Postels & Ruprecht; G after Reinke; the rest after Skottsberg.)

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it is always only the outer segment that undergoes further development (cf. fig. 74 D, E). The splits soon commence to appear nearer the inner margin of this segment (fig. 74 C) and as a result a relatively narrow piece (*bl*) gets detached from the large remaining part (*t*). The latter, gradually assuming a falcate shape, comes to occupy a terminal position (fig. 74 D, E, *t*) on the elongating sympodial stipe and constitutes a formative tract from which segments are detached unilaterally in a single series (fig. 74 C). The opposite margin of this terminal blade soon thickens to form a keel (*k*) ((193) p. 805) which is continuous with the stipe below. Along its edge lies the meristematic zone, the region of maximum growth being located at the point of transition between the blade and the stipe. As successive segments become detached, the intervening parts of the keel elongate to form "internodes" (*i*) whereby the individual blades become spatially separated. According to Brandt ((18) p. 40) a frond lives for 4–7 months. Loose-lying forms are recorded in New Zealand ((216) p. 338).

The development of *Macrocystis*, like that of *Lessonia*, is therefore effected by successive splitting of the primary blade, but of the two segments thus formed in *Macrocystis* one remains arrested, while the other (the outer) continues to develop; the successive pedicels of the favoured segment combine to form a sympodial stipe which bears the other, narrower segments along its inner side (fig. 74 A, D, E). Before the segments of the functional blade become free (fig. 74 C), the basal portions enlarge to form the air-bladders (*b*), while the short stalks of the blades (*p*) develop subsequently. Surface-growth of the blades continues for some time and leads to the characteristic corrugation, while the two-ranked arrangement is due to a subsequent readjustment. In robust plants other long shoots may arise by the further development of some of the first-formed inner segments.

The sori ((29), (66), (68) p. 62, (179) p. 104, (182)) are usually formed on the blades of short forked shoots arising at the base of the plant and remaining deeply submerged. These fertile shoots do not exhibit the one-sided development that characterises the sterile ones, and in habit they are much like one of the smaller species of *Lessonia*. Sori, however, also occasionally occur on the ordinary blades at the water-surface ((179) p. 105); in either instance they lie mainly in the furrows.

It is not without interest to compare *Macrocystis* and *Nereocystis*. In the former the primary stipe remains quite short, while its branches unite to produce sympodial stipes of great length. In *Nereocystis*, on the other hand, it is the primary stipe that continues to grow, whilst the forks themselves remain quite short. In the former, flotation is secured by a bladder at the base of each blade, in the latter by a single bladder at the summit of the main stipe.

Pelagophycus ((9) p. 6, (65), (164), (171); *Nereocystis gigantea* Aresch. (7), (35) p. 7), confined to a small part of the coast of California, has a habit rather like that of *Nereocystis*. The stipe, usually 6–10 metres

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long, is surmounted by a large spherical air-bladder, beyond which it forks into two equal horizontal arms, each bearing at intervals 4–6 delicate secondary blades attached by slender stalks and reaching a length of 6 metres. The blades are formed by unilateral splitting of the two primary blades in much the same way as in *Macrocystis* and form the sori ((65) p. 345) at their tips. Large individuals are stated to reach a length of 45 metres ((42) p. 475).

A

B

Fig. 75. A, *Macrocystis* and B, *Egregia Menziesii* (Turn.) Aresch., low tide, Monterey Peninsula, California. (Photos F. E. Fritsch.)

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The monotypic and perennial *Lessoniopsis* ((54) p. 9, (134) p. 25; *Lessonia littoralis* Farl. & Setch. (106)) is distinguished from other Lessoniaceae by the differentiation of fertile and sterile blades (fig. 76 F). The former (*f*) are broad and oval, with a sharply demarcated stalk, and bear the sori (*so*) on both surfaces. The sterile blades (*v*), on the other hand, are narrow and strap-shaped and merge gradually into the stalk. They are usually provided with an ill-defined midrib (fig. 76 C, *r*) and segment by the formation of repeated splits (*sl*) through the latter, whereas the fertile blades show no division. These sporophylls ((55), (176) p. 632) are outgrowths from the stalks of the sterile blades and develop in pairs from the transition region year after year. The short firm, often deeply furrowed, stipe bears at its summit numerous branches, produced by successive splitting, as in *Lessonia*; older plants may bear as many as 800 blades ((106) p. 320). Like *Postelsia*, *Lessoniopsis* grows above low-tide limit in situations exposed to strong surf, although it usually occurs at a lower level than the former.

The Family Alariaceae

The series of forms included in this family are, like *Lessoniopsis*, characterised by the restriction of the sori to special sporophylls, but the ordinary vegetative fronds do not here undergo splitting. The sporophylls arise as outgrowths, either from the stipe or from the margin of the blade. The young plants are again of the *saccharina* type (fig. 76 D).

The most familiar member of this family is *Alaria* (158, 206), the main centre of distribution of which appears to be in the Arctic and the Northern Pacific, although a number of species are found in the North Atlantic. Of these, *A. esculenta* ((64) pl. 79), popularly called Badderlocks or Henware, is not uncommon in exposed situations near low-water mark, though usually growing submerged. All species of *Alaria* are perennial. The relatively short stipe (fig. 76 E, *st*) bears an elongate lamina, which often possesses a wavy margin (cf. fig. 76 A) and is decurrent on to the stipe; the blade is traversed by a stout midrib (*r*) which appears as an upward continuation of the stalk. During summer the latter produces in acropetal succession near its upper end two rows[1] of thick tongue-shaped sporophylls (fig. 76 A, E, *s*) which, after the maturation of their sori, are shed during autumn and winter, leaving small scars on the stipe. At this time of the year the blade becomes torn into segments perpendicular to the midrib (fig. 76 G, *ob*) and ultimately wears away more or less completely; fresh growth in the transition zone early in the following season leads to its replenishment (cf. below). New sporophylls sprout out above those of the preceding season.

[1] The rows are sometimes double in *A. esculenta*, according to Sauvageau ((156) p. 223).

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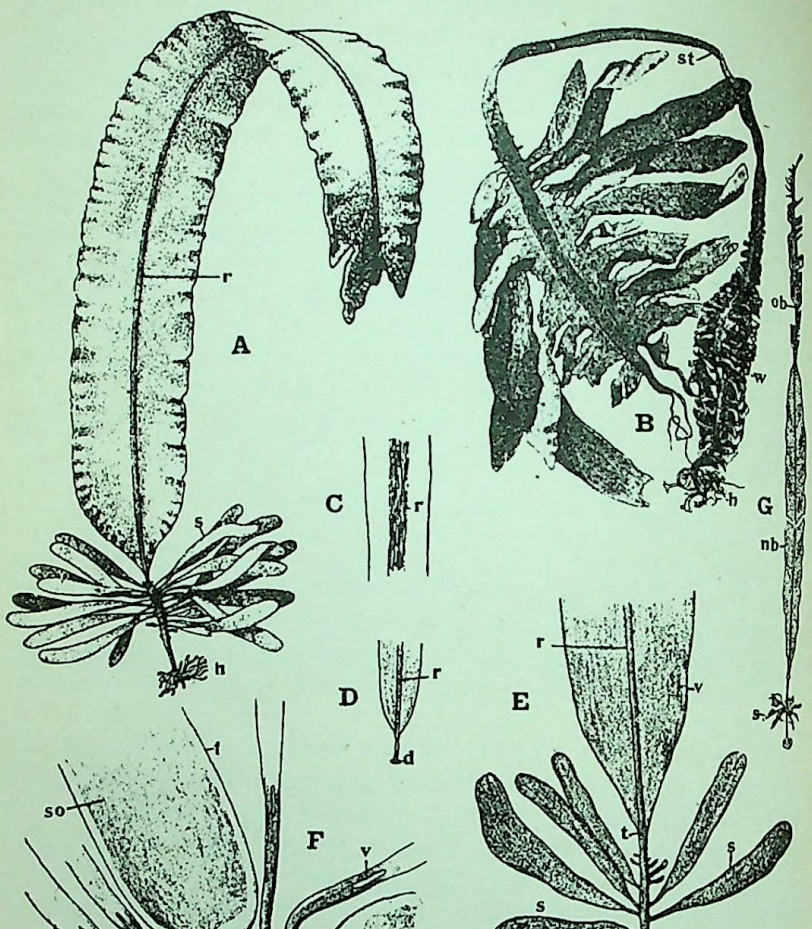

Fig. 76. A, *Alaria oblonga* Kjellm., habit. B, *Undaria pinnatifida* (Harv.) Kjellm. C, F, *Lessoniopsis littoralis* (Farl. & Setch.) Reinke; C, upper part of a vegetative blade; F, small part of a mature plant. D, E, G, *Alaria esculenta* (L.) Grev.; D, lower part of young plant; E, basal part of older plant; G, blade renewal. *f*, fertile blade; *h*, hapteron; *nb*, new and *ob*, old blades; *r*, midrib; *s*, sporophyll; *sl*, slit; *so*, sorus; *st*, stipe; *t*, transition zone; *v*, vegetative blade; *w*, wing. (A, B after Kjellman; C–F after Reinke; G after Rasmussen.)

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The mode of renewal of the lamina in *A. esculenta* and other species seems to take place somewhat differently in different localities. Thus, on Scandinavian shores ((9) p. 16, (129) p. 195, (195) p. 7) the old blade wears away almost completely before the new one is formed and in the last months of the year the lamina is represented by the remains of the midrib. On French and British shores, on the other hand, as well as in other regions ((131), (142) p. 113, (206) p. 49), renovation of the lamina takes place more as in *Laminaria*, since here the old blade persists until the new one has grown to a considerable size (fig. 76 G). Various authorities ((14) p. 450, (16), (42) p. 481, (125), (156) p. 221) affirm that growth in the transition zone is continuous and that the blade is replenished basally in the same measure as it wears away apically. According to Yendo (206) the Japanese *Alarias* last for only two years.

The midribs and sporophylls of *A. esculenta*, which have a sweet insipid taste, were occasionally consumed in the seventeenth century in parts of Scotland (184), while in Kamschatka the midribs of *A. fistulosa* are eaten ((206) p. 58). The blade of the former may reach a length of 6 metres ((183) p. 283), although the stipe does not exceed 30 cm.; the sporophylls may be 25 cm. long, with a width of about 2 cm. The largest species appears to be the North Pacific *A. fistulosa* Post. & Rupr. ((126) pl. 16), with blades up to 25 metres long and as much as 230 cm. wide ((42) p. 481, (175) p. 275, (176) p. 644, (206) p. 12); the midrib is in great part hollow, its successive chambers being separated by partitions composed largely of hyphae (78). The species of *Alaria* favour habitats exposed to surf (183) and Macmillan (108) describes forms of *A. nana* Schrader which, in their short sturdy habit, recall the *Postelsias* with which they are associated.

Some species (*A. marginata* Post. & Rupr.) have relatively large sporophylls and in this respect approach the monotypic *Pterygophora* ((9) p. 11, (104) p. 114, (107), (144) p. 73, (172) p. 96). Here (fig. 77 A) the long woody stipe (*st*), rounded at the base but gradually flattening above, bears sporophylls (*s*) reaching a length of 1½ metres and forming sori largely at their base. The terminal blade (*v*), which may likewise become fertile, is not much longer than the sporophylls. It is often in large part disintegrated, although, as in *Alaria*, it may subsequently regenerate from the base. New sporophylls are produced in each season above those of the preceding year.

In *Undaria* (*Ulopteryx* ((86) p. 274, (118), (186) p. 77, (204) p. 704; figs. 76 B; 77 C), the species of which are confined to Japan (see map 2, p. 252), the lower part of the lamina bears pinnately arranged outgrowths, whilst the flattened stalk is provided with an undulate wing (*w*) upon which the sori are produced. To this genus Okamura (118) refers *Laminaria Peterseniana* Kjellm. ((86) p. 267, (117) p. 98), as well as Yendo's (201) genus *Hirome*. The latter (fig. 77 B) is distinguished by the fact that sori (*so*) are also developed on the blade. Sauvageau ((156) p. 4) suggests that it may be a hybrid. Yendo ((206) p. 73) considers that the genera *Hirome*, *Undaria*, *Alaria*, and *Pterygophora* form a series in which the production of special fertile zones or sporophylls from the stalk becomes progressively more marked.

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The systematic position of *Phyllogigas* ((45) p. 47, (179) p. 63; *Lessonia simulans* Gepp (47), (48) p. 5) in which the secondary blades that sprout out from the stipe are altogether like the terminal blade, is uncertain, since so far only sterile plants have been found.

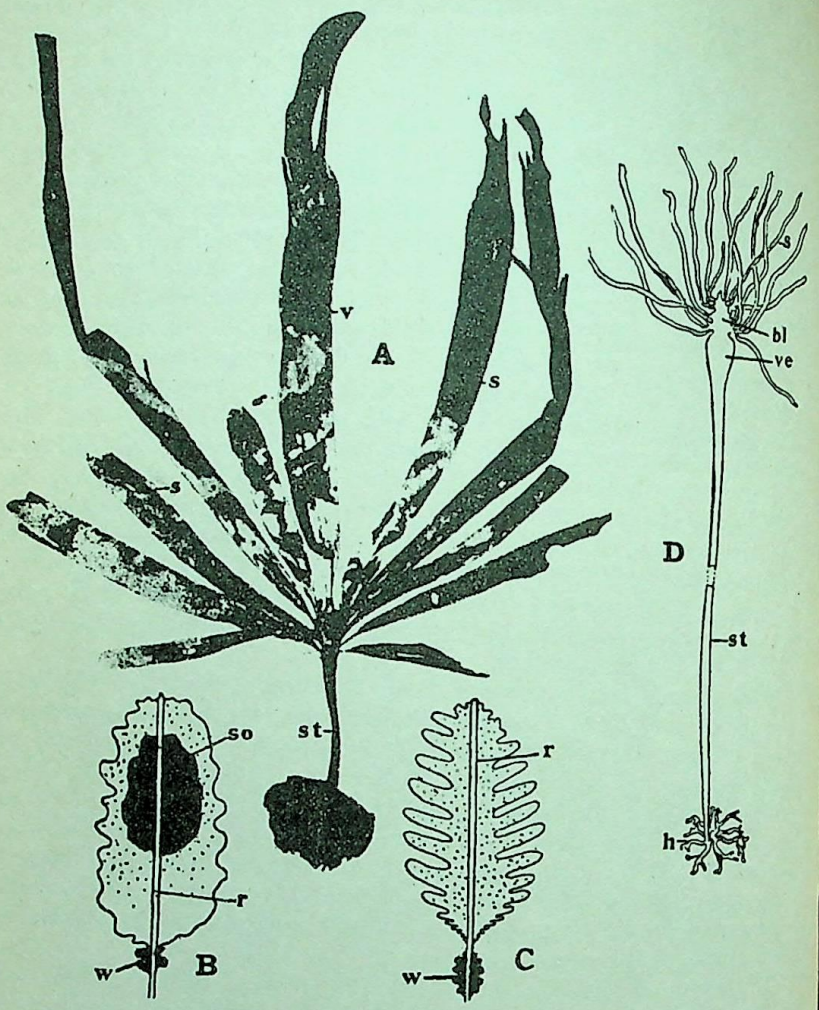

Fig. 77. A, *Pterygophora californica* Rupr., habit. B, *Hirome* sp., diagrammatic representation of a plant. C, *Undaria* sp., ditto. D, *Ecklonia buccinalis* (L.) Hornem. *bl*, blade; *h*, hapteron; *r*, midrib; *s*, sporophylls; *so*, sorus; *st*, stipe; *v*, vegetative blade; *ve*, air-bladder; *w*, wing. (A after Setchell & Gardner; B, C after Yendo; D after Delf.)

In other Alariaceae the sporophylls arise as marginal pinnations of the lamina. In the Californian *Eisenia arborea* ((7) p. 68, (9) p. 7, (146) p. 431, (163), (165), (170), (200)) they appear already in the young plant (fig. 78 B) and, whilst the apex of the primary blade (fig. 78 C, *b*)

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gradually wears away, the pinnae themselves (*s*) enlarge and become as big or even bigger than the main blade. At this stage the lower margins (*l*) of the latter become inrolled and, as this happens, the enclosed margins thicken (cf. *Hedophyllum*, *Arthrothamnus*, p. 200).

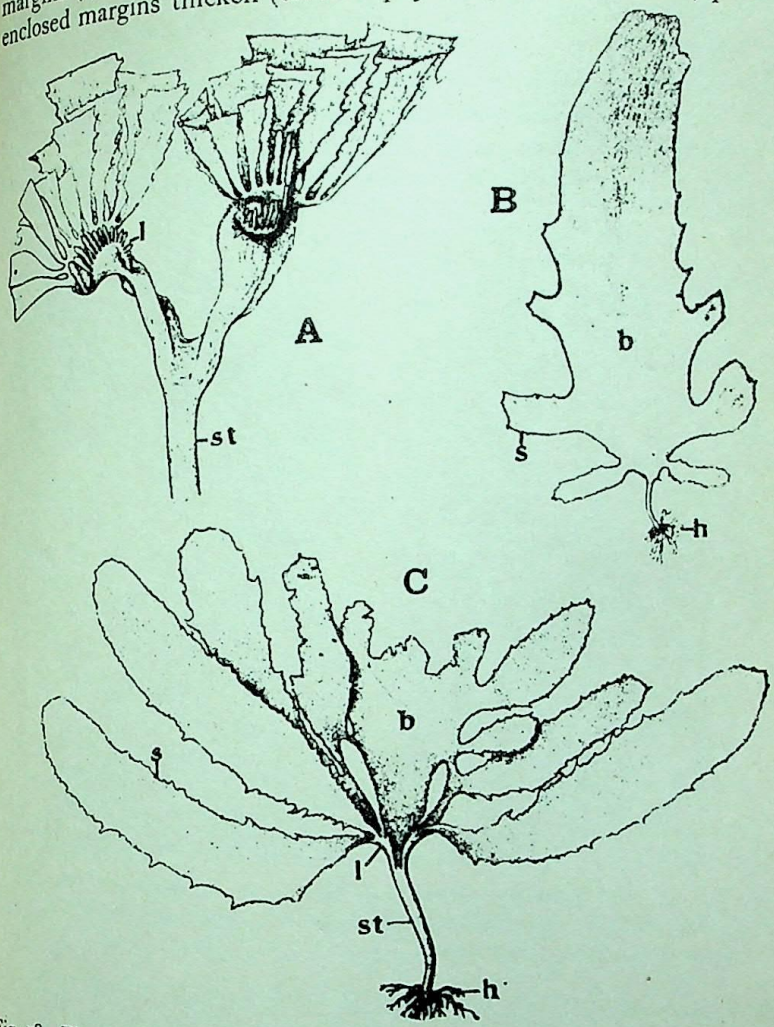

Fig. 78. *Eisenia arborea* Aresch. (after Setchell). A, incurving of margins of primary blade; B, young plant; C, older stage, with well-developed pinnae. *b*, vegetative blade; *h*, hapteron; *l*, inrolled basal margin of blade; *s*, sporophyll; *st*, stipe.

Ultimately, when the primary blade has worn down to its very base, the involuted margins constitute two arms at the top of the stipe (fig. 78 A). The formation of pinnae is now transferred to secondary meristematic zones at the tips of these arms, but the original meristem persists at the top of the stipe which continues to grow in length. It becomes a stout and fairly rigid structure flattened near the top.

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The sori form elongate patches on the basal parts of the sporophylls. Another species, *E. Cokeri* Howe ((68) p. 55), recorded from Peru, is only doubtfully distinct ((67) p. 34), but a further characteristic form is the Japanese *E. bicyclis* (Kjellm.) Setch. ((119) pl. 238, (170) p. 128, (200); *Ecklonia bicyclis* Kjellm. (86) p. 269), in which the sporophylls may themselves be pinnate.

The species of *Ecklonia* ((9) p. 12, (116), (187)), principally represented in the Southern Hemisphere (see map 2, p. 252), are well illustrated by *E. buccinalis*[1] (fig. 79 A), the Bamboo Seaweed of South Africa ((27), (126) pl. 2, (213)), which somewhat resembles *Nereocystis* in habit (cf. also

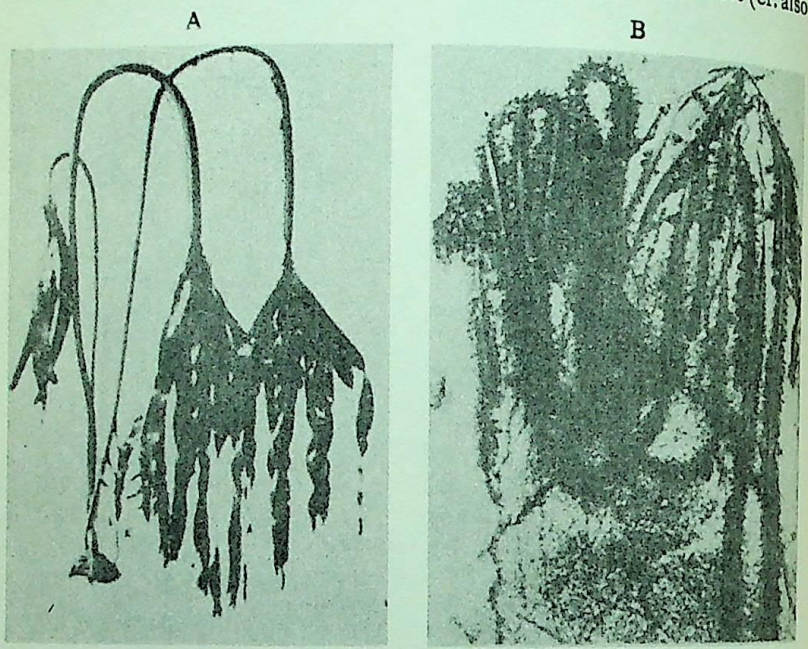

Fig. 79. A, *Ecklonia buccinalis* (L.) Hornem., 1/20 natural size (photo: M. A. Pocock). B, *Egregia Menziesii* (Turn.) Aresch. (photo: F. E. Fritsch, Monterey Peninsula, California).

fig. 77 D), although the numerous blades are produced in quite a different manner. The hollow erect stalk, which may be 5 or more metres in length, enlarges at its summit (*ve*), but the primary lamina (*bl*) remains small and the greater part of it often wears away. The basal portion, however, persists and from it there grow out in acropetal succession numerous long narrow sporophylls (*s*) bearing irregular sori. Some species propagate by stolons ((119) pl. 140). Young plants (fig. 79 A, *g*) show resemblance to those of *Eisenia*.

The greatest elaboration among Alariaceae is attained by *Egregia* ((7) p. 66, (9) p. 3, (115), (130), (144) p. 70), the species of which form

[1] According to Papenfuss ((213), p. 16) the correct name of this species is *E. maxima* (Osbeck) Papenf.

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extensive meadows at and below low-water mark on the western coasts of North America (fig. 75 B). Young plants of *E. Menziesii* ((54) p. 17) are of the customary type (fig. 80 C), but at an early stage short flat ligulate segments (*l*) sprout out from the lower margins of the blade (*b*) and from the flattening stipe (*st*). The intercalary meristem contributes but little to the enlargement of the blade which ultimately wears away completely, whilst the flattened stalk (fig. 80 A, *st*) exhibits continuous elongation, at the same time producing more and more lateral outgrowths (*l*).

The considerable branching is effected mainly from the basal parts of the thallus, where some of the outgrowths develop into long shoots (fig. 80 A, *br*). These likewise bear numerous marginal appendages and may grow to a length of more than 8 metres (fig. 79 B). Cylindrical at the base, they are markedly flattened (fig. 80 A, *f*) throughout the greater part of their length and, in older plants, numerous perforations often appear in these band-shaped structures, while they are densely covered with blunt papillae (*p*). The short laterals function as photosynthetic organs, and in *E. laevigata*, found in Lower California, vary from simple linear blades to pinnate structures with filiform segments (fig. 80 D). Here and there the base of one of the laterals swells up to form an air-bladder (fig. 80 A, B, *a*). Those that function as sporophylls (fig. 80 D, *sp*) are wrinkled pod-shaped structures bearing the sori between the ribs.

Except for the somewhat aberrant genus *Chorda*,[1] the diverse seaweeds surveyed in the preceding pages all appear as post-embryonal modifications of a central type resembling such a form as *Laminaria saccharina* (54, 134). Subsequent elaborations are due, on the one hand, to progressive splitting affecting either the lamina only and leaving the meristem intact (Laminariaceae) or extending also into the region of the latter with a resulting segregation of the same into numerous separate entities (Lessoniaceae), the latter process admitting of especially striking developments. On the other hand, in the Alariaceae, elaboration is largely due to the development of outgrowths from the stipe or lamina, such outgrowths being frequently diverted

[1] *Adenocystis* ((45) p. 43, (60) p. 179, (61) p. 218, (62) pl. 48, (83), (95) p. 305), a common Antarctic littoral form ((214) p. 59), with a stalked vesicular thallus of no considerable dimensions (fig. 71 G), was referred by Kjellman ((85*a*) p. 255) to Laminariaceae, while Oltmanns ((122) p. 66) includes it in Encoeliaceae and Skottsberg ((179) p. 39) in a special group Adenocystideae among Ectocarpales. Young stages, described by the last ((180), p. 40), show considerable resemblance to those of *Chorda*; they possess an apical hair, later replaced by a group of hairs sunk in a depression ((113) p. 62). Somewhat older plants are much like a young *Laminaria*. The mature thallus forms an almost continuous sorus of unilocular sporangia with intervening paraphyses. A very similar form described by Skottsberg ((179) p. 6, (180) p. 42) as *Utriculidium*, bears plurilocular sporangia; should his suggestion that the latter may represent the sexual generation of *Adenocystis* prove to be true, a reference to Laminariales is clearly out of the question.

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to reproductive functions. The splitting of the lamina, as well as the perforations that occur in more than one evolutionary series, are no doubt adaptations admitting of the production of a large photosynthetic surface capable of resisting the rough seas to which the thalli are often exposed. The elaborate holdfasts (fig. 65 N), with pro-

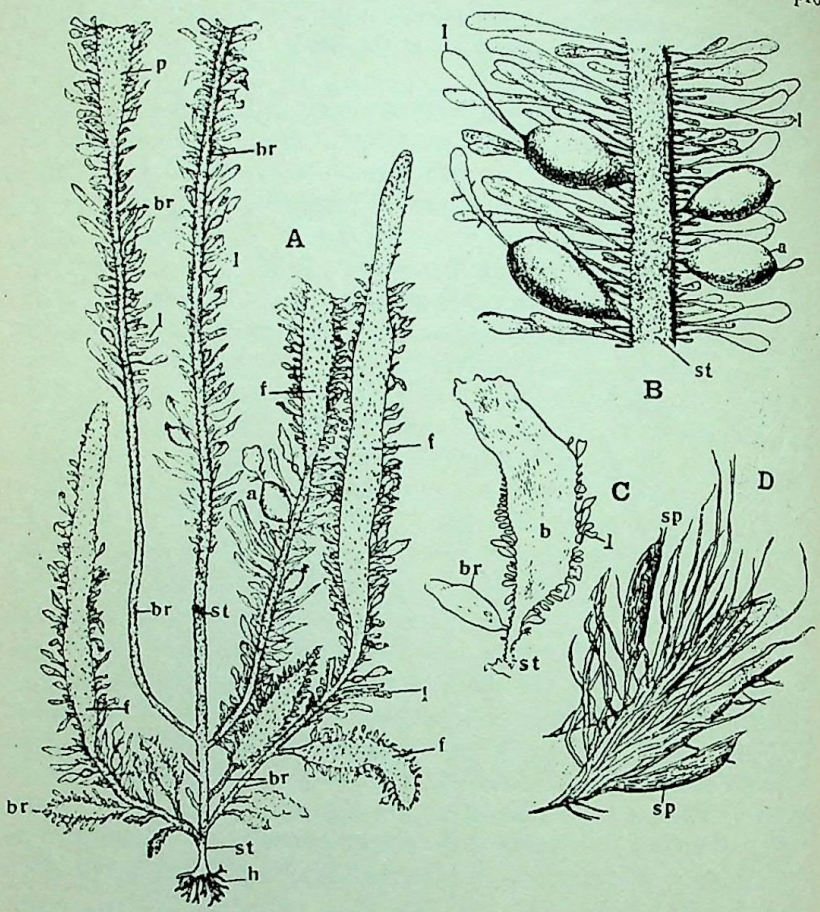

Fig. 80. *Egregia Menziesii* (Turn.) Aresch. A, basal part of older plant; B, part of a branch enlarged; C, young plant; D, part of a branch with sporophylls (*E. laevigata*?). *a*, air-bladder; *b*, primary blade; *br*, branch; *f*, flattened region of branch; *h*, hapteron; *l*, lateral; *p*, papillae; *sp*, sporophyll; *st*, stipe. (A, C after Fallis; B, D after Reinke.)

duction of increasing numbers of branched haptera as the thallus enlarges, are well suited for anchorage in such a habitat, while the strong, though flexible, construction of the stipes (cf. below) admits of display of the blades to the best advantage.

Before proceeding to consider the internal structure, certain features of the growth of Laminariales may be noted. Elongation of

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the stipe and much of the enlargement of the lamina are due to the meristematic region in the transition zone, but, apart from annual forms with a long stipe (*Nereocystis* (32), (39)), the growth of the latter is inconsiderable compared with the increase of the lamina. In a perennial *Laminaria*, *Alaria*, etc. the greater part of the stalk consists of mature tissue, except in so far as there may be secondary activity leading to increase in thickness (p. 232). In the latter part of the season most of the lamina, too, is no longer enlarging, but during and soon after the time of blade-renewal an extensive basal region is in vigorous growth and further additions to the base of the blade may be made from the transition zone during the whole of the vegetative season. With the approach of winter this activity is arrested and it is then as a rule that the sori are produced (cf. also (30) p. 178).

The growth of the stipe of *Nereocystis* is very rapid, about 2·5 cm. per day during July (177) and probably more than that in younger stages ((39) p. 144). According to Fallis (33) the maximum growth of the blade in *Laminaria*, *Alaria*, *Costaria*, etc. takes place in the widest part near the base. The rate increases rapidly for a short distance above the base and beyond that again decreases. The rate of growth during the day is almost double that at night. The average daily growth recorded by Fallis is 2·85 cm. in *Laminaria*, 2·23 cm. in *Alaria*, and 2·04 cm. in *Costaria*, these increments being largely due to the lengthening of the blades. According to Sauvageau ((156) p. 205) *Chorda filum* can reach a length of four metres in 4 months, while growth of the new blade of *Laminaria Cloustoni* ((156) p. 190) is estimated at 0·5 cm. per day and plants of this species can reach a height of one metre in the first year ((210) p. 328). Lemoine ((102) p. 5) found in young plants of *L. saccharina* a growth of only 2·4–3·7 cm. and in older ones of 2–5·2 cm. per month, but on the Welsh coast plants reach a length of 30 cm. in less than 3 months. The breaking strain of the stipes is considerable ((28), (73) p. 193) and plants are often detached complete during storms ((80) p. 493).

THE ANATOMICAL STRUCTURE OF THE SPOROPHYTE

(*a*) CHORDA

The zygotes of *Chorda* ((6) p. 15, (77) p. 108, (93) p. 25, (94) p. 72, (133) p. 37), like those of other Laminariales, divide transversely to produce a short thread (fig. 81 B–E, *e*), the basal cell of which lengthens into a rhizoid (*r*). A distinctive feature lies in the appearance of one or more apical hairs (fig. 81 F, G, *h*), which may develop while the embryo is still a simple filament. The first longitudinal walls (fig. 81 F, G) arise in planes at right angles to one another and divide the upper cells into quadrants; this is followed by transverse division and subsequently by the formation of radial and tangential longitudinal walls. Meanwhile a large number of the lower cells grow out into septate rhizoids (fig. 81 H, *r*).

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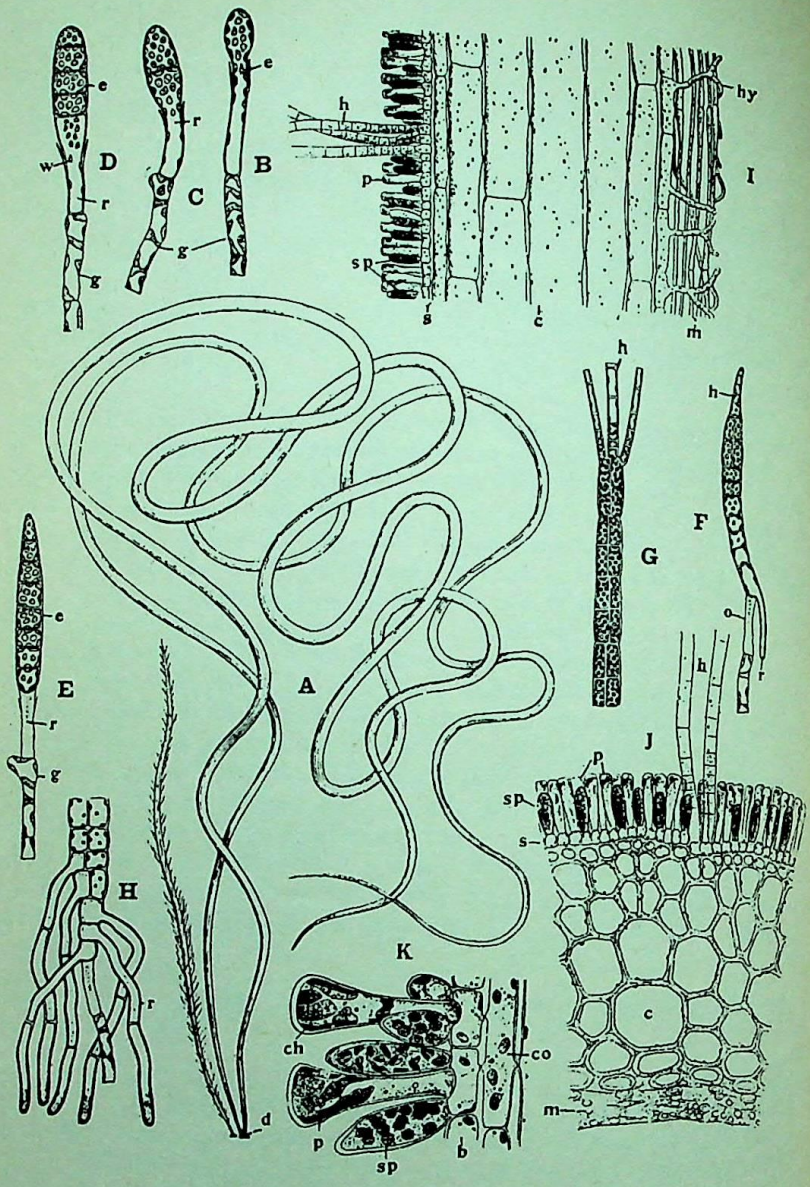

Fig. 81. *Chorda filum* (L.) Lamour. A, habit; B–F, young plants of successive ages, still attached to the gametophyte (*g*); G, apex of a somewhat older plant; H, base of ditto; I, part of longitudinal and J, of transverse section of mature thallus; K, small part of a sorus in longitudinal section. *b*, basal cell; *c*, cortex; *ch*, chromatophore; *co*, cross-connection; *d*, attaching disc; *e*, embryo; *g*, gametophyte; *h*, hair; *hy*, hyphae; *m*, medulla; *o*, oogonium; *p*, paraphysis; *r*, rhizoid; *s*, surface-layer of thallus; *sp*, sporangium; *w*, wall of oogonium. (A after Newton; B–H after Kylin; I–K after Reinke from Oltmanns.)

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The parenchymatous cylinder thus produced at first shows little differentiation, but soon a transverse meristematic zone is established near the top of the germling ((93) p. 27). By its activity new tissue is added both above and below throughout the summer, although that above the meristem dies away sooner or later. Sections through the meristematic zone display a central group of cells formed from the original parenchymatous cylinder and a wide outer zone with radially arranged elements which no doubt originate by repeated tangential division of the surface-layer (meristoderm, cf. p. 226). Below the meristem the surface-cells undergo abundant anticlinal division, while the inner cells fail to divide and become more or less pronouncedly elongated. The marked surface-enlargement is probably directly responsible for the development of the central hollow.

In sections of the mature thallus ((93), (133) p. 35; fig. 81 I, J) the surface-layer (*s*) of isodiametric or palisade-like cells, with abundant chromatophores, is followed by one or two layers, the cells of which, though almost equally narrow, are markedly elongate. The greater part of the wall of the hollow thallus is, however, composed of wide elongate cells (*c*), which become narrower towards the interior. Here this cortex suddenly gives place to a system of very narrow elongate threads (*m*), which exhibit the characters of "trumpet-hyphae" (p. 231). A quantity of ordinary hyphae (*hy*) arise from the inner cells of the cortex and, growing mainly in the horizontal direction, extend into the hollow; they become aggregated at fairly even intervals to form bridging diaphragms. The hyphae are stated to contain chromatophores ((74) p. 19). At intervals the surface of the thallus bears tufts of colourless hairs (*h*).

The central hollow contains mucilage and gases which may cause local inflations. The marked tensile strength of the thallus is ascribed by Pringsheim (127) to the wide cortical cells, the walls of which exhibit two sets of striations, visible at a different focus and accompanied by slit-shaped pits. The inner striations give the inner margin of the wall a furrowed contour, while the outer ones are due to undulation of the surface of the inner layers. When a piece of the thallus is allowed to dry, it becomes markedly contorted, so much so that it may appear 8-shaped in section.

(*b*) The early Development of other Laminariales

The embryonic stages have been studied in numerous Laminariales[1] and in general show considerable uniformity. The zygotes commonly germinate while still adhering to the empty oogonium (fig. 82 B, C, I, *o*), which is often perforated by the first rhizoid. The lengthening zygote undergoes transverse septation to produce a short erect thread

[1] See (18) p. 4, (30), (76), (79), (92) p. 558, (104) p. 128, (128), (147), (154), (156), (204) p. 692, (213) p. 18.

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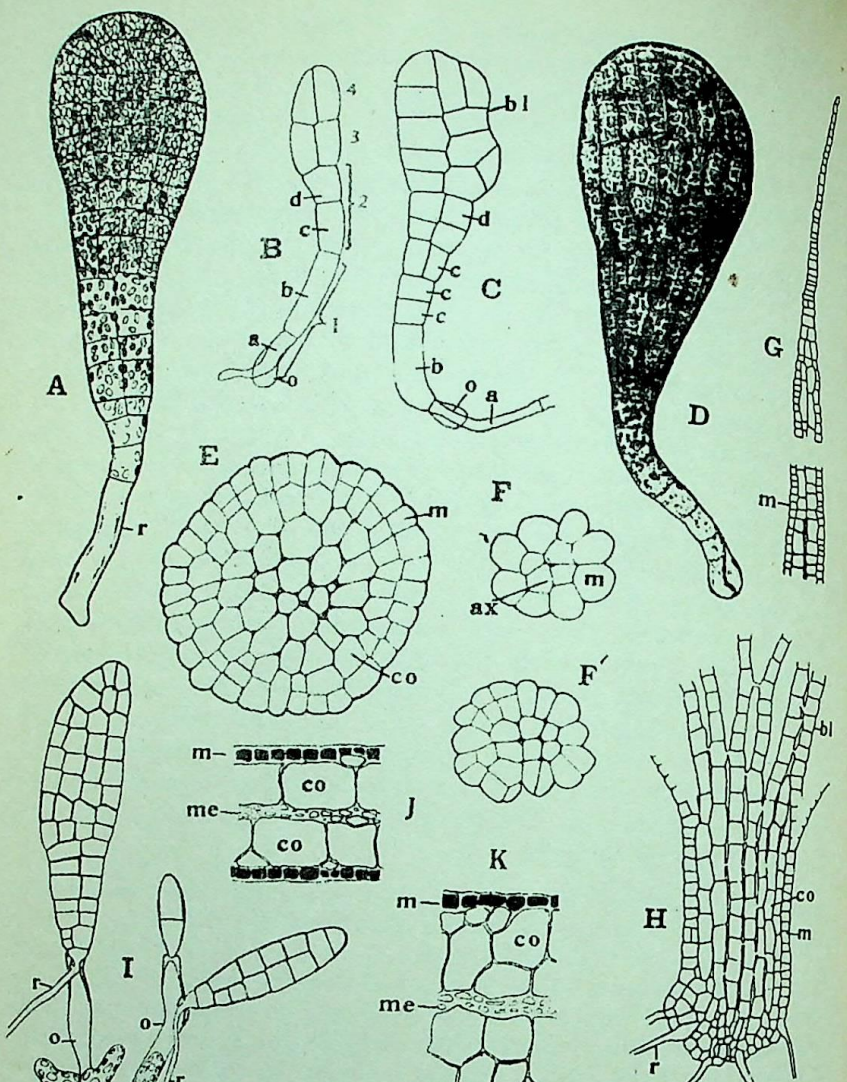

Fig. 82. Early development of Laminariales. A, *Costaria costata* (Turn.) Saund., germling. B–F′, L, *Saccorhiza bulbosa* De la Pyl.; B, C, early segmentation of germling, 1–4 in B the first-formed cells, those marked *a–d* equivalent in B and C; D, older germling; E, F, F′, transverse sections at progressively higher levels through the stipe in the order F, F′, E; L, transverse section through the blade of a young plant. G–I, *Laminaria digitata* (L.) Lamour.; G, longitudinal section through young blade; H, longitudinal

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(fig. 90 A, Q, *em*), the cells of which divide by longitudinal walls chiefly orientated in the vertical direction (fig. 82 A–D, I); this results in a flat one-layered expanse which is usually broader above than below. The first rhizoid is soon supplemented by others emanating from the lower cells of the germling. The rhizoids may be septate ((156) p. 59) or non-septate ((204) p. 696, (213) p. 19); in *Alaria* (128) they are branched.

The polarity of the young plants of *Egregia* is determined by the direction of the incident light (115), while according to Williams (198) the filamentous embryos are positively phototropic. Longitudinal division may set in at an early stage ((128) p. 14) or a uniseriate filament of 6–8 cells may first be formed ((156) p. 153). According to Yendo ((204) p. 693) the filamentous embryos of *Costaria* show apical growth.

Sauvageau ((156) p. 56) describes a definite sequence of division in *Saccorhiza bulbosa* (fig. 82 B). The two uppermost cells (*3*, *4*) of the four-celled thread first produced undergo longitudinal septation to form the one-layered apex of the young blade (fig. 82 C, *bl*), while the two lower ones (*1*, *2*) exhibit a further transverse division. The basal cell (*a*) develops into a rhizoid, the next above (*b*) furnishes the lower part of the future stipe, the uppermost (*d*) produces the basal part of the young blade, while the third from below (*c*) gives rise to the intercalary meristem of the transition zone. So clear a differentiation does not appear to occur in the embryos of other Laminariales.

Sooner or later longitudinal walls are formed also in other planes in the basal part of the embryo, whereby the cylindrical stipe is initiated (fig. 82 F, I); meanwhile abundant division is taking place in the region of the lamina which, however, for some little time usually remains monostromatic. Meristematic activity now begins to concentrate at the base of the lamina (transition zone) and from then onwards plays an important part in the further enlargement of blade and stipe ((156) p. 59, (204) p. 695). The meristematic zone is at first only a transverse row of cells, but it soon becomes more extensive. Over an increasing area of the central portion of the blade, extending outwards from the transition zone, the lamina becomes first two-, then three-, and then four-layered (cf. fig. 82 G). Both marginal and apical regions, however, appear usually to remain one-layered, at least for a considerable length of time ((30) p. 186, (156) p. 73, (161) p. 198, (204) p. 698). Various authorities ((51) p. 660, (79) p. 447, (156) p. 64, (195) p. 28) state that the young blade possesses a marginal meristem which

section through a young germling in a plane parallel to the surface of the blade; I, germlings of various ages, still attached to the gametophyte. J, K, *Macrocystis pyrifera* (Turn.) Ag., transverse sections of young blades. *ax*, axial cells; *bl*, blade; *co*, cortex; *m*, meristoderm; *me*, medulla; *mu*, "cellule multiclave"; *o*, oogonium; *r*, rhizoid; *s*, solenocyst. (A after Yendo; D after Thuret; G, H after Killian; J, K after Skottsberg; the rest after Sauvageau.)

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contributes to its enlargement,[1] but there is also appreciable surface-growth effected by crosswise anticlinal division of the cells of the two superficial layers ((156) p. 64), while the inner ones enlarge to keep pace with this growth (cf. fig. 82 L).

The early development of the stipe has been followed by Sauvageau ((156) p. 99) in *Saccorhiza bulbosa*. After the primary cells have divided into quadrants, periclinal walls (fig. 82 F) cut off a peripheral layer (*m*) from a central group of cells (*ax*), which show no further division and constitute the first medullary elements. The peripheral layer, however, remains actively meristematic, segmenting by anticlinal, and especially by periclinal, walls (fig. 82 E, F′) and giving rise to a cortex (*co*) from which further additions are progressively made to the medulla (cf. below); by degrees the inner cells develop thick mucilaginous walls (cf. also fig. 82 H). The surface-layer of actively dividing cells may appropriately be designated by the name of *meristoderm* proposed by Sauvageau ((156) p. 99).

(*c*) The Structure of the Stipe[2]

In transverse or longitudinal sections of an older stipe of a *Laminaria* or *Alaria*, taken at or near the transition zone, it is generally possible to distinguish four regions (fig. 83 A; cf. also fig. 86 B). At the surface is the actively dividing *meristoderm* (*m*) just considered, followed internally by one or more layers of similar small cells. The meristoderm is covered by a mucilage-layer (*mu*) occupying the position of a cuticle. Internal to this small-celled tissue follows an *outer cortex* (*oc*) of somewhat wider and paler cells, which are markedly elongate, but show no pronounced thickening of the wall; the cells commonly have pointed ends and exhibit frequent horizontal septa. Further to the interior lies the *inner cortex* (*ic*), the cells of which are longer and have square ends, while the longitudinal walls show increasing gelatinisation; the cells of this region, too, exhibit numerous horizontal thread-like outgrowths (cross-connections and hyphae, *hy*; cf. below). The centre of the stipe is occupied by a mass of tangled threads, constituting the *medulla* (*me*), which is commonly oval or elliptical in cross-section (see fig. 85 N). It is not possible to draw a

[1] In the young frond of *Laminaria Lejolisii* Sauvageau ((156) p. 173) describes a group of apical cells, the activity of which is, however, limited to the formation of the mucronate tip which here crowns the young blade. The growth of the young lamina in *Costaria costata* is, according to Yendo ((204) p. 695), due to the division of two initial cells situated beneath the apical cap.

[2] See (51) p. 657, (105) p. 284, (107) p. 734, (111), (122) p. 154, (126) p. 7, (132), (138) p. 113, (161) p. 196, (179) p. 116, (181) p. 573, (188) pp. 299, 309, (195) p. 11. I have also through the kindness of Dr J. W. G. Lund been able to consult a manuscript containing preliminary results of his investigation of the structure of *Laminaria*.

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hard and fast limit between the different regions, since they grade over into one another.

When active growth is proceeding, the cells of the meristoderm at the level of the transition zone have a palisade-like shape (fig. 83 C, I, *m*) and exhibit frequent tangential septation, with simultaneous radial divisions so that the cells remain small. They contain numerous small chromatophores and evidently constitute a photosynthetic layer. The cells cut off internally rapidly widen to form the outer cortex and lengthen, often assuming a more or less spindle-shaped form (fig. 83 D) and, since there is no corresponding increase in chromatophores, the cells appear paler. The elongation of these cells is often accompanied by the appearance of a number of thin horizontal septa (*s*) so that each cell gives place to a vertical row.

Towards the interior of this tissue (fig. 83 E, K) the longitudinal walls commence to thicken and there is a gradual passage to the inner cortex. The thickening is due to mucilage, which is stated to be formed from the middle lamella ((188) p. 300). The vertical files of cells constituting the inner cortex (fig. 83 A, *ic*) thus become separated by increasingly wide tracts of mucilage, except at certain points where there is no gelatinisation (fig. 83 D, K, L, *p*); these pits are often in the main situated on the tangential walls ((194) p. 67). As the inner cells separate more and more, the pits between them become horizontally extended and form short cross-connections which may become septate (fig. 83 E, K, *co*). This mode of formation of cross-connections has been described by several investigators ((138) p. 115, (161) p. 200, (193) p. 804, (195) p. 12).

According to Killian ((79) p. 450; cf. also (138) p. 116), however, such structures are only of a temporary nature and most of the numerous *cross-connections*, seen in the inner cortex and the medulla, arise by the fusion of papillose protrusions (fig. 84 A, B, *p*) formed at corresponding levels on the longitudinal walls. These outgrowths originate from small cells cut off by an oblique septum at the upper end of the parent-cell, although later most of them come to lie opposite the horizontal walls between successive cells (fig. 84 A, *p*). These structures grow towards one another (fig. 84 B) until they meet and thereupon elimination of the separating walls takes place just as in a process of conjugation (fig. 84 C, *co*), although there is no fusion of nuclei. The cross-connections thus formed elongate in the same measure as the vertical rows of cortical cells separate and, as this happens, the former undergo septation (figs. 83 F, *co*; 84 E, G, *co*).

Meanwhile, as the inner cortex is supplemented from the outer, its innermost elements are added to the medulla, while further contributions are made to the outer cortex by the operation of the superficial meristem. Continuous formation of new cross-connections takes place in the inner cortex so that at its inner limit and in the region of

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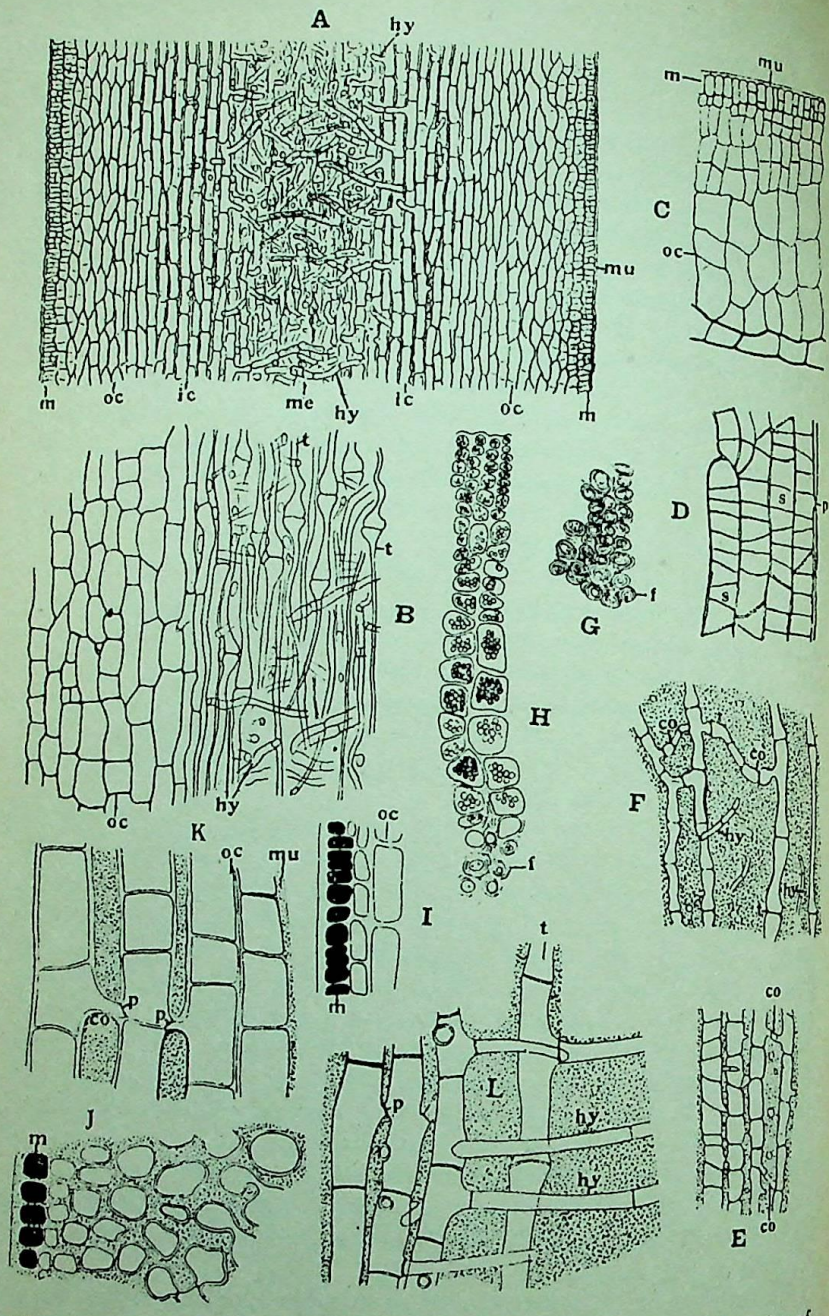

Fig. 83. Structure of the stipe. A, *Laminaria* sp., longitudinal section of young stipe. B, *Eisenia arborea* Aresch., ditto. C–F, *Macrocystis pyrifera* (Turn.) Ag., successive parts, from without inwards, of a longitudinal section below the transition zone, C at right angles to the other three; C, meristoderm and outer cortex; D, inner cortex; E, edge of medulla; F, medulla. G, H,

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the medulla a complete longitudinal network is produced (fig. 84 G). The mode of origin of cross-connections described by Killian is also reported by Sauvageau ((156) p. 123) in *Saccorhiza*, but it remains to be established whether it is of general occurrence among Laminariales.

Somewhat later there begins the development of the structures known as *hyphae* ((161) p. 201, (195) p. 14), which differ essentially from the cross-connections only in the absence of fusion with a corresponding outgrowth.[1] Hyphae can apparently grow out directly from the cells of the inner cortex (fig. 83 L), but, according to Killian ((79) p. 454), those of *Laminaria* arise, like the cross-connections, from small cells cut off in the middle of the cortical elements. The hyphae develop into slender, often branched ((122) p. 154, (193) p. 806) threads of considerable length, which grow mainly in the radial direction into the copious mucilage of the medulla (fig. 83 A, B, *hy*). Here they commonly pursue a tortuous course so that it is difficult to trace them to their full extent.

The medulla thus includes structures of three different kinds, viz. (*a*) medullary cells (fig. 83 B, F, L, *t*) derived from the innermost elements of the cortex and arranged in more or less evident longitudinal rows; (*b*) cross-connections (*co*), primarily horizontal but later often pursuing an oblique course; and (*c*) the numerous hyphae (*hy*) which extend in all directions between the others, though prevalently radial. It is by no means always easy to distinguish these diverse elements from one another. Surface-enlargement and increase in width are taking place continuously in the transition zone and below it, so that there is a passive extension of the medullary cells and of their cross-connections, in both of which the capacity for growth is sooner or later lost. Since they undergo no further septation, the component cells are drawn out, and this is accompanied by a reduction in width except at the septa, where the original dimensions are maintained. Many of the medullary elements consequently exhibit a characteristic widening at the septa (fig. 83 A, B, F, *t*), which is responsible for the customary designation of these structures as

[1] The statements that the hyphae can fuse with other elements ((188) pp. 300, 309, (195) p. 20) remain doubtful.

Lessoniopsis littoralis (Farl. & Setch.) Reinke, transverse sections; G, thick-walled cells (*f*) at periphery of medulla; H, entire sector. I–L, *Alaria esculenta* (L.) Grev., sections through the transition zone, J, transverse, the others longitudinal, the mucilage dotted; I, J, meristoderm and outer cortex; K, beginning of inner cortex; L, edge of medulla. *co*, cross-connection; *hy*, hyphae; *ic*, inner cortex; *m*, méristoderm; *me*, medulla; *mu*, mucilage; *oc*, outer cortex; *p*, pit; *s*, septate cortical cell; *t*, trumpet-like enlargement. (A after Oltmanns; B after Killian; C–F after Rosenthal; G, H after Macmillan; I–L after Wille.)

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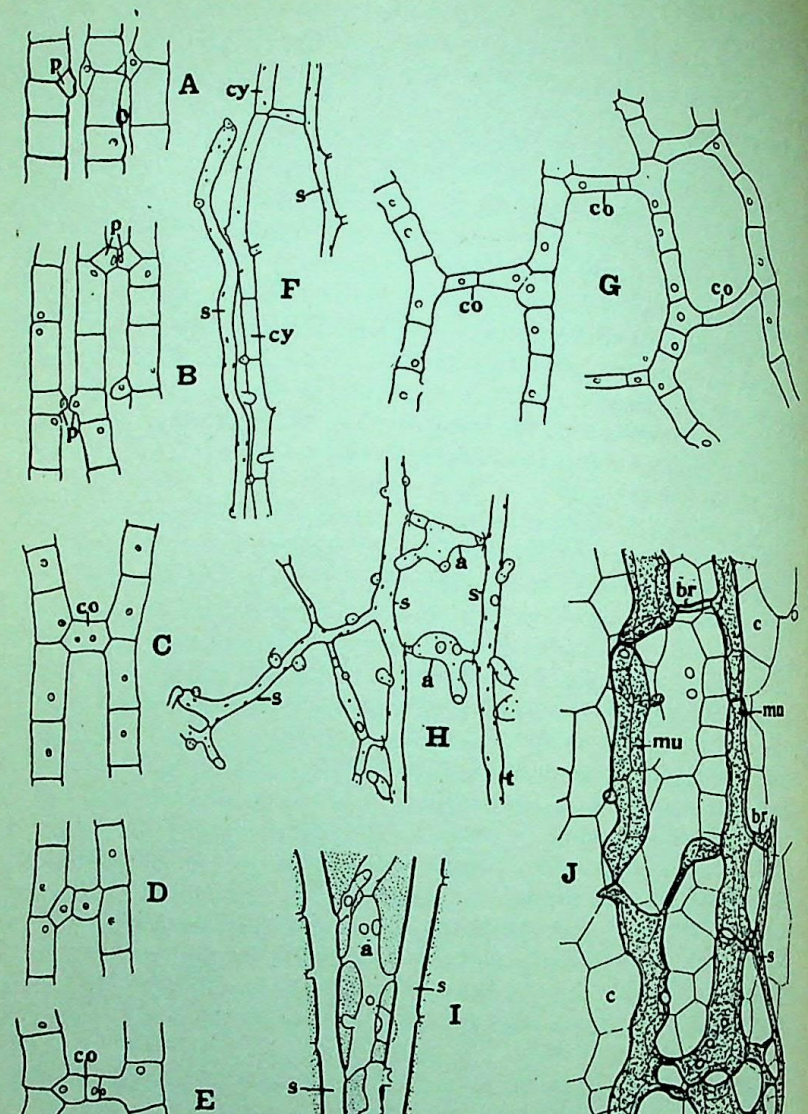

Fig. 84. A–E, G, *Laminaria digitata* (L.) Lamour., origin (*p*) and development of cross-connections (*co*) (after Killian). F, H–J, *Saccorhiza bulbosa* De la Pyl., details of medullary elements (after Sauvageau). *a*, "allelocysts"; *br*, branch; *c*, cortical cell; *cy*, "cylindrostyles"; *mu*, "cellules multiclaves"; *s*, "solenocysts"; *t*, constrictions on the latter.

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trumpet-hyphae; it appears, however, that the actual hyphae only rarely give rise to these elements. The surface-enlargement, leading to passive distention of the internal elements, often results in marked tensions between the outer and inner tissues; strips cut out of a fresh stipe become curved with the outer surface on the convex side ((195) p. 13).

The cells cut off internally by the meristoderm of the young stipe (fig. 82 E) show the characteristics of outer cortical cells, but, as these lengthen in relation to the surface-growth and more elements are added by the meristoderm, the innermost exhibit thickening of the longitudinal walls and develop cross-connections; in this way the inner cortex is initiated. With further widening of the stipe and outgrowth of hyphae from the inner cortical cells, the medulla begins to differentiate, and thus the young stipe acquires the series of intergrading tissue-regions that in later stages is met with especially in the transition zone. In the older plant increments to the various tissues appear to be made essentially only in this zone, since the primary regions above distinguished decrease in size as one passes for instance down the stipe of a *Laminaria*. The medulla seems to undergo little or no increase below the level of the transition zone and in the maturer parts there is usually a sharp boundary between it and the cortex (cf. (51) p. 647, (179) p. 70, (188) p. 302) (fig. 83 B). Increase in width of the stipe is here due to some further additions to the outer cortex, but mainly to special secondary activity (p. 232). It is not clear whether there is continued production of hyphae from the cells of the inner cortex in the older parts of the stipe, but this would appear to be so in certain instances ((79) p. 460).

The meristem of the transition zone is therefore of such a nature that it gives rise progressively to the various tissues of the stipe in a horizontal direction and, where such differentiation ceases, there is little further increase in length and the tissues are essentially mature. Fallis' data (p. 221) indicate that the region of elongation and differentiation is normally rather limited. The formative region of the stipe is, however, continuous with that of the lamina and there is no interruption of tissues in passing from the one to the other; the medulla in particular extends throughout the whole transition zone. This is probably the explanation why, despite the existence of an active meristem in this region, there is no mechanical weakening at the level of the transition zone. The latter differs appreciably from the maturer parts above and below only in the more gradual transition between cortex and medulla and in the marked evidence of elongation and horizontal septation in the outer cortical cells. In the more mature parts several layers of small cells with chromatophores commonly occur beneath the meristoderm ((195) p. 17).

In certain Laminariales (e.g. *Macrocystis* ((138) p. 116, (179) p. 119; *Lessoniopsis* (106) p. 329) the meristoderm appears to remain in

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operation throughout life, but in *Laminaria* ((132) p. 377), *Lessonia* ((51) p. 647), *Thalassiophyllum* ((138) p. 141), *Alaria* ((37) p. 20), and *Nereocystis* ((105) p. 288, (121) p. 100), for example, meristematic activity is subsequently transferred to a cortical layer, situated at a depth of about 4–8 cells beneath the surface. This secondary meristem brings about progressive increase in thickness of the outer cortex and the numerous cells it produces exhibit a radial arrangement. This secondary growth is responsible for the considerable thickness attained by the older stipes of *Lessonia* and of some *Laminarias*. The primary tissue towards the outside usually dies and is shed.

In the perennial forms the activity of the secondary meristem is periodic and the wide outer cortex that is gradually produced usually shows a concentric zoning recalling the annual rings of higher plants (fig. 85 N); although clearly apparent to the naked eye, the rings[1] are often difficult to distinguish under the microscope. Their formation in *Laminaria* ((100), (122) p. 159), *Pterygophora* ((107) p. 735, (181) p. 577) and *Lessonia* ((51) p. 647) appears to depend on periodic differences in the colour of the cell-contents and the size of the cells, whilst in *Thalassiophyllum* (143) they are due to differences in the colour and thickness of the walls of the secondarily formed elements. It is still a matter of debate whether the successive rings represent annual increments. For the *Laminarias* of the Norwegian coast Printz ((129) p. 186) relates them to the annual renewal of the blade and believes that each represents a year's growth (cf. also (100) p. 553, (106) p. 326). Others (160) have brought them into relation with the formation of successive series of haptera.

In the mature stipe the horizontal walls of the inner cortical cells usually show a number of pits which are commonly arranged in a ring (fig. 85 M, O) near the periphery ((138) p. 127, (181) p. 577, (188) pp. 303, 312); the pit-membranes are stated to be traversed by delicate cytoplasmic connections and similar plasmodesmae are reported in the septa of the hyphae and of the cross-connections ((194), (195) pp. 19, 48). Church ((22) p. 77) records numerous pits on the tangential walls in the secondary cortex. In the medulla and in the parts of the inner cortex immediately adjacent to it the cross-walls show a fine sieve-like pitting which is often very evident on the septa of the young trumpet-hyphae (fig. 85, L); such structures are often referred to as sieve-tubes. According to Sykes ((188); cf. however (181) p. 583) the young septum is traversed by numerous cytoplasmic threads (fig. 85 J), exhibiting a varied arrangement; in the older ones each thread becomes converted into a slime-string enclosed in a rod of callus.

Sieve-tubes of a more distinctive type are found in the inner cortex of *Macrocystis* and *Nereocystis* (fig. 85 I; (105) p. 287, (121), (179) p. 119,

[1] Macmillan also describes rings in *Lessoniopsis* ((106) p. 327) but here they appear in tissue formed from the meristoderm.

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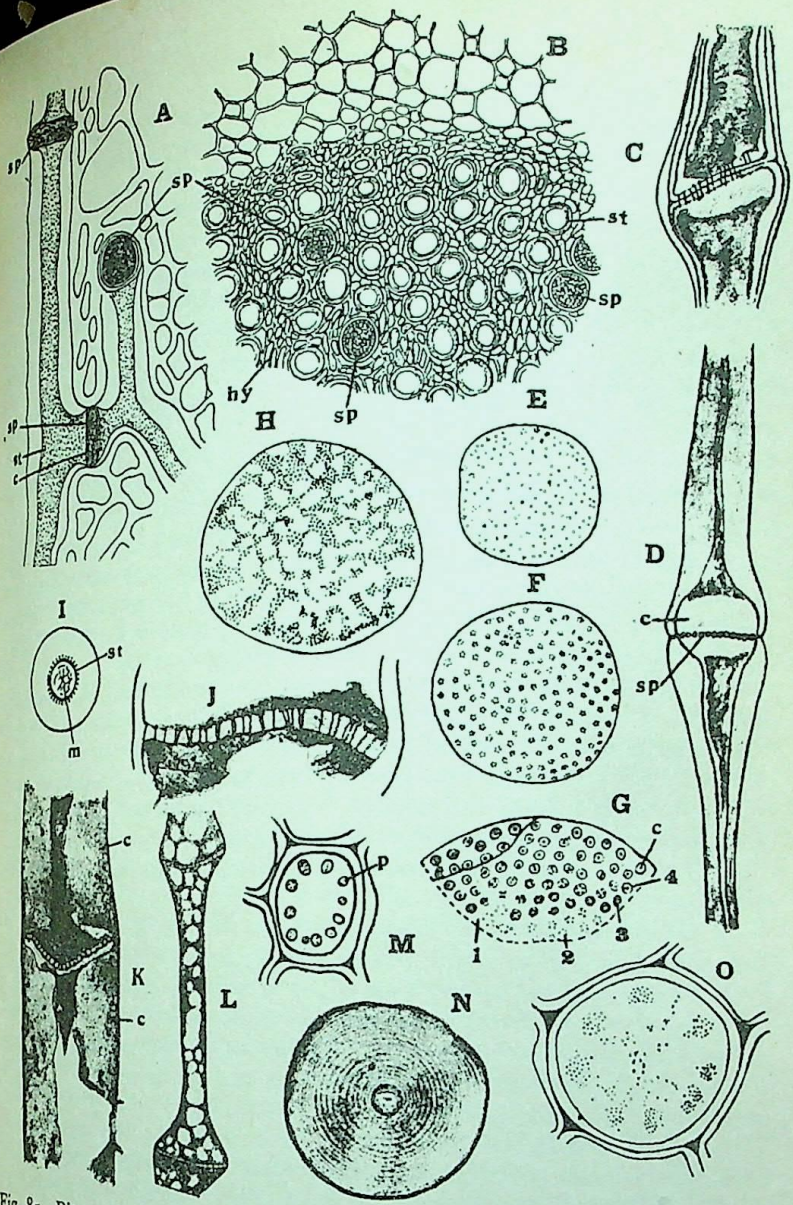

Fig. 85. Pits and sieve-tubes of Laminariales. A–G, J, K, M, *Macrocystis pyrifera* (Turn.) Ag.; A, longitudinal section of inner cortex, with sieve-tubes; B, transverse section through inner cortex; C, young sieve-tube; D, older trumpet-hypha with much callus; E, F, two stages in development of a sieve-plate; G, part of a sieve-plate showing four stages (1–4) in the development of the pores; J, section of a young sieve-plate showing cytoplasmic threads, partly in groups; K, old sieve-tube, callus-deposit on side-walls; M, cross-section of cortical cell, showing the septum. H, O, *Laminaria saccharina* (L.) Lamour.; H, sieve-plate from inner secondary sieve-tube; O, transverse section of inner cortical cell showing the septum. I, *Nereocystis Luetkeana* (Mert.) Post. & Rupr., diagram of cross-section of stipe showing position of sieve-tubes (*st*). L, *Alaria esculenta* (L.) Grev., trumpet-hypha. N, *Laminaria Cloustoni* Edmonds., transverse section of stipe showing growth-rings. *c*, callus; *hy*, hyphae; *m*, medulla; *p*, pit; *sp*, sieve-plate; *st*, sieve-tube. (A after Oliver from Oltmanns; B after Will; I after Macmillan; L after Wille; N after Foslie; the rest after Sykes.)

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(193) p. 825), and it might be better to restrict the name to these structures. In transverse sections (fig. 85 B) they appear as large and rather thick-walled elements (*st*) which are arranged in more or less distinct radial rows and are surrounded by dense masses of hyphae (*hy*); the septa are differentiated as typical sieve-plates (*sp*) perforated by coarse pores. These structures do not show the widening at the septa that characterises the trumpet-hyphae of the medulla (fig. 85 A). In general they pursue a longitudinal course, although neighbouring ones are linked by short cross-connections, the septa of which are likewise differentiated as sieve-plates. The considerable width and specialisation of the cortical sieve-tubes of these two genera is perhaps to be related to the great length attained by the slender stipes which necessitates conduction over a long distance ((121) p. 113).

According to Sykes (188) "sieve-tubes", similarly disposed in radial rows, occur also in the inner cortex of *Laminaria saccharina* and probably of other species. These structures, however, exhibit neither the large size, nor the well-differentiated sieve-plates found in the sieve-tubes of *Macrocystis* and *Nereocystis*; in fact, except for the absence of marked inflation at the septa, they resemble the trumpet-hyphae of the medulla. There can be little doubt that all these structures are homologous with one another and that, in the older parts of the stipes where no further additions to the medulla are being made, "sieve-tubes", which have not been drawn out like the trumpet-hyphae, are differentiated in the inner cortex. It would seem, however, that this formation of extramedullary sieve-tubes is limited to the innermost region of the cortex.

In *Macrocystis* (188) the young sieve-plate (fig. 85 E) shows essentially the same features as the septa of the trumpet-hyphae. Later each primary cytoplasmic connection divides to form a group (fig. 85 F), each member of which forms its own callus-rod. Still later the individual strands of a group fuse to form a single slime-string (fig. 85 G; 1–4 are successive stages), and in this way the coarse pores of the sieve-plates are produced.

Both in the cortical sieve-tubes and in the trumpet-hyphae of the medulla the older septa become obliterated by deposits of callus (fig. 85 A, D, *c*; (121)). This appears to take place centrifugally, since the medullary elements show such deposits at a time when the cortical ones exhibit few traces of them. In older trumpet-hyphae callus may be deposited almost throughout (fig. 85 K). The elements, which are thus obliterated, usually have appreciably thickened walls, the thickening consisting mainly of cellulose.

Both the trumpet-hyphae of Laminariales as a whole and the sieve-tubes of *Macrocystis* and *Nereocystis* are no doubt conducting elements, which according to Rigg (136) are specially concerned with the transport of protein (cf. however (12)). Wille (194, 195) regards the cells of the cortex as storage and mechanical elements, and it is possible that in the young stipe they furnish the chief strengthening system (cf. also (28)). In the older plant, however, mechanical elements are principally located in the

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medulla and the adjacent parts of the inner cortex and it is no doubt these which are responsible for the marked tensile strength of the stipes ((155) p. 756). The oval medulla of the mature stalk of *Alaria esculenta* ((195) p. 21) consists exclusively of strongly thickened cells. In *Saccorhiza dermatodea* Setchell ((161) p. 204) records, at the periphery of the medulla, a layer of fibre-like, thick-walled elements (between 3·2 and 7·5 cm. long) which can be removed from the other tissues by maceration and extends without interruption through the transition zone from stipe to blade. Analogous structures occur in *S. bulbosa* ((156) p. 119) and *Pterygophora* ((107) p. 736), while a similar distribution of mechanical elements appears to obtain in *Lessoniopsis* ((106) p. 327; fig. 83 G, H, *f*) and to a less marked extent in *Cymathere* ((53) p. 91). These mechanical elements of the mature stipe are probably in most, if not in all, instances the trumpet-hyphae of younger stages which have become extremely attenuated, have undergone very extensive thickening of their walls, and have in part become filled with callus. Such changes are recorded in *Alaria* (195), *Nereocystis* (105), *Macrocystis* and *Laminaria* (188). The medulla of *Costaria* ((181) p. 579) consists of nearly isodiametric cells.

Sauvageau's detailed description (156) of the anatomy of *Saccorhiza bulbosa* at various stages of development (cf. also (155)) differs in certain respects from the accounts given for other Laminariales, and it is not altogether clear whether the differences are peculiar to this species or are the outcome of differences in interpretation. According to him (pp. 102, 116) the medullary cells ("solenocysts") multiply, already in the young stipe, by the formation of outgrowths which extend both in the upward and downward directions and enlarge until they reach the width of the parent-cells; they may produce others in the same way. These medullary elements (fig. 84 F, H, *s*), which may attain a great length and only rarely branch, are multinucleate and possess but few septa, although they show occasional constrictions (*t*); they are regarded as conducting elements (p. 124). Other outgrowths ("allelocysts", pp. 104, 122), which arise from the medullary cells (cf. (10) p. 54), remain short (fig. 84 H, I, *a*) and appear to correspond to the hyphae and cross-connections (p. 123) of other investigators. In the medulla of the blade Sauvageau (p. 120) distinguishes longitudinal elements called "cylindrostyles" (fig. 84 F, *cy*), composed of a number of elongate, thin-walled, multinucleate cells with few chromatophores; they are believed to arise from the "solenocysts". There can be no doubt that a comparative investigation of the histological structure of a number of Laminariales would furnish results of interest.

(*d*) The Structure of the Lamina

The mature lamina ((181) p. 581) shows the same basic structure as the stipe, but, owing to the great surface-enlargement, the elements of the medullary region are drawn out in all directions (fig. 87 E, *me*) and do not show the prevalently longitudinal course which is characteristic of the stipe. Moreover, except where special ribs are developed, the inner elements exhibit a relatively loose aggregation.

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The medulla occupies a rather narrow tangential zone, which is bounded on either surface by a cortex (*ic*, *oc*) composed of a limited number of cell-layers; the inner cortex is often not clearly differentiated. The network of medullary cells and cross-connections found in the young blade (fig. 82 H, *bl*) soon loses its regularity as the latter enlarges. The rows of medullary cells are dragged out of their longitudinal course (cf. fig. 84 G), while many of the cross-connections are so much displaced that they may even come to run longitudinally (⟨79⟩ p. 452); in the older blade it is practically impossible to distinguish the two kinds of structures. In *Alaria* (⟨195⟩ p. 28) the medullary elements are mainly orientated at right angles to the midrib so that the blade tends to tear in this direction. Except in the midribs and other thickened parts, hyphae are not nearly as abundant as in the stipes; they exhibit a far more irregular course.

The early stages in the development of the blade have again been specially studied in *Saccorhiza bulbosa* by Sauvageau (⟨156⟩ pp. 98, 107, 109). According to him periclinal division of the surface-layer only takes place exceptionally (cf. also ⟨132⟩ p. 373, ⟨195⟩ p. 29). The meristematic region at the base of the blade—at first merely a single layer (cf. p. 225), later composed of two and then of four or more layers—furnishes by the anticlinal division of the cells the successive layers forming the cortex of the blade. The cells of the superficial layer divide crosswise by frequent anticlinal walls, whilst the subjacent layer or layers, which owe their origin to the meristem of the transition zone and not to division of the surface-layer, merely enlarge to keep pace with this surface-growth. Yendo (⟨204⟩ p. 696) reports essentially the same in *Costaria*.

The mode of origin of the medulla is scarcely clear. Sections of young blades, after the four-layered condition has been attained, show a central system of elongate elements (fig. 82 J, K, *me*) which exhibit no direct relation to the peripheral layers and afford no satisfactory evidence of origin from the latter (cf. ⟨161⟩ pp. 195, 205, ⟨179⟩ p. 123, ⟨204⟩ pl. 55, figs. 43, 44). Drew (⟨30⟩ p. 187) and Killian (⟨79⟩ p. 449) describe how the older germlings of *Laminaria* exhibit the gradual spread, from the transition zone upwards into the blade, of a dark area (fig. 65 G, H, *m*) marking the appearance of the first medullary elements within the latter. This is in agreement with Sauvageau's investigations (⟨156⟩ pp. 106, 115), according to which the medulla in the blade of *Saccorhiza* originates by the upward extension through the now elliptical transition zone of medullary cells ("solenocysts") from the young stipe, their prolongations spreading out fan-wise within the mucilage between the cortical layers on the two surfaces of the blade. These observations furnish an explanation for the sharp contrast that is often evident, both in younger and older stages, between the cortex and medulla of the lamina. Sauvageau (p. 107) states that the blade is always thicker at the base than above and this fact,

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which is also true of *Laminaria*,[1] agrees with a penetration from the stipe of tissue-elements, which at a higher level, as a result of the rapid widening of the blade, become spread out between the cortical layers. A repetition of Sauvageau's observations on *Saccorhiza* and other Laminariales is obviously indicated. The medulla does, however, also receive additions from the cortex of the developing blade, although the extent of such contributions is at present unknown. In *Saccorhiza* Sauvageau ((156) p. 109) describes the ingrowth of cortical cells into the medulla, the gap thus created in the cortex being filled by periclinal division of the surface-layer. The elements thus added to the medulla ("cellules multiclaves", fig. 82 L, *mu*) are multinucleate and become very long without developing septa (cf. fig. 84 J, *mu*); they produce numerous short and narrow branches (*br*) by means of which they communicate with one another, as well as with other elements of the cortex and medulla.

Hairs are not as frequent as in most other orders of Phaeophyceae, but they occur on the blades of various genera (*Alaria* ((113), (195) p. 36; *Saccorhiza* (113), (161) p. 202; *Nereocystis* (105) p. 291; *Costaria* (204) p. 701; *Undaria* (204) p. 706). They are colourless and show the customary basal growth, usually forming tufts, which in later stages commonly occupy shallow pits owing to rapid growth of the surrounding cells. Dyes penetrate very rapidly into these hairs ((195) p. 37). In *Saccorhiza* ((156) p. 116) the tufts often arise opposite the enlarged termination of a medullary cell ("solenocyst") which, according to Sauvageau, is continuous from the stipe into the blade. In *Alaria* and *Nereocystis* the hairs disappear in the mature plants.

In conclusion we may endeavour to form a general picture of the growth of a *Laminaria* or other similar, not markedly modified, member of Laminariales. The seat of active cell-division is doubtless in the vague region known as the transition zone which is usually approximately circular in section at the top of the stipe, but more or less markedly elliptical at the base of the lamina. At periods of active growth the surface-layer in this region is undergoing copious division, both anticlinal and periclinal. In passing to the maturer parts of the stipe division of this meristoderm gradually ceases. In the blade, however, it continues to take place abundantly, although it is entirely or almost entirely anticlinal, so that great surface-enlargement occurs. The region of active cell-division in the transition zone is a hollow, and probably for the most part one-layered, cylinder which surrounds a core of mature or maturing tissue. All the cortical layers of the blade and young stipe are furnished from corresponding layers of the

[1] According to Lund (see footnote on p. 226) the considerable thickness of the basal part of the older lamina is due to a great development of the cortical region. He also finds that the new blade of *Laminaria* is thicker than the old (cf. however (167) p. 118) and that, as the former enlarges, it becomes progressively thinner. This is almost entirely due to a decrease in the thickness of the medulla.

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transition zone. The medulla of the blade arises *pari passu* with that of the stipe, as the first-formed medullary cells elongate in the upward and downward directions within the transition zone. It may well be that there is no direct extension of the medulla into the blade, but that, as additions are made to the four-layered base of the lamina, the latter acquires a medulla of elongate cells in the same measure as such a medulla differentiates in the transition zone. This picture endeavours to reconcile the diverse data to be found in the literature; how far it corresponds with the actual state of affairs only detailed observations on living plants can show.

(*e*) Mucilage-canals ((57), (138) p. 124, (193) p. 803)

Mucilage-canals, which form an anastomosing system in the outer cortex, are met with in the stipes and blades of several Laminariales,[1] in certain species of *Laminaria* (*L. saccharina*, *L. digitata*) and in *Nereocystis* and *Cymathere* ((181) p. 581) they occur only in the blades. As a general rule the canals of the stipe are arranged in a single layer in transverse section, but in *L. Lejolisii* ((25) p. 105), as well as in *L. Cloustoni*, they may form two rings ((156) pp. 161, 186), while in the older stipe of *Macrocystis* there are several concentric series ((179) p. 119). They are invariably situated on the outside of the secondary meristem above described. In the laminae the canals constitute separate systems on the two faces.

In *Laminaria* ((57), (156) p. 179) the mucilage-canals develop schizogenously at the upper and lower ends of the transition zone, and this is no doubt true also of other Laminariales. They first appear between the surface-cells as narrow slit-shaped spaces (fig. 86 B, *s*), which are radially elongated and, as a result of the division of the meristoderm (*m*), gradually come to occupy a deeper position; as this happens, they widen and become spindle-shaped. A few millimetres beyond the transition zone the mucilage-cavities undergo tangential enlargement and, as a result, they fuse with one another, both in the transverse and longitudinal directions, to form a continuous network (fig. 86 C), which varies considerably in the shape and size of the meshes ((57) p. 27). Simultaneously they become protruded on their outer side (fig. 86 A) and extend into the meristoderm, commonly penetrating to the surface, where they may even cause slight prominences; there is, however, no evidence of a direct connection with the external medium.

At the inner margin of the mucilage-cavities, not far beyond the place of their first formation, there appear small cells with a large nucleus and abundant granular cytoplasm (fig. 86 B, *e*). These multiply

[1] Mucilage-canals are lacking in *Saccorhiza*, *Alaria*, *Pterygophora*, *Pleurophycus*, *Thalassiophyllum*, *Egregia*, *Costaria*, *Dictyoneurum*, as well as in some species of *Laminaria* (e.g. *L. Agardhii* Kjellm.).

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by division and gradually constitute an irregular layer over the inner surface of the space (fig. 86 A, *e*). In longitudinal sections, however, it is seen that these cells form isolated groups (fig. 86 C, *e*) and,

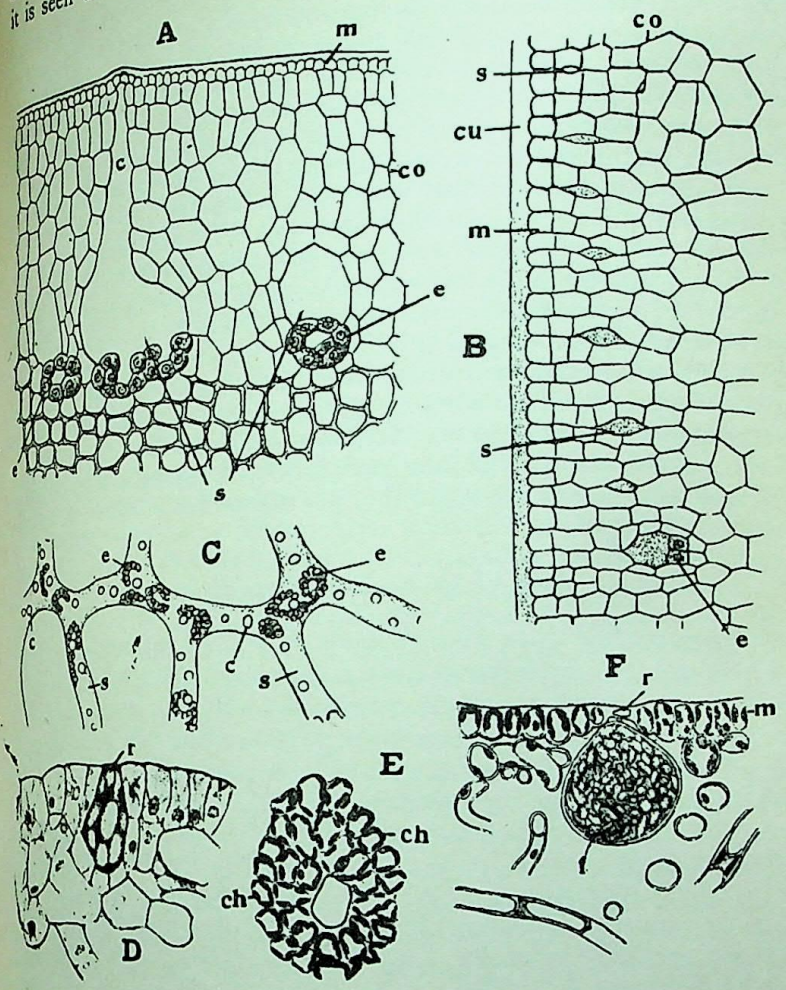

Fig. 86. A–C, *Laminaria Cloustoni* Edmonds., mucilage-canals (after Guignard); A, in a transverse section of the stipe; B, in a longitudinal section through the transition zone; C, small part of the network, as seen in a tangential section of a young blade. D–F, *Undaria pinnatifida* Sur., var. (after Yendo), fucosan-cells; D and F, in section, D young; E, surface-view. *c*, protuberance of mucilage-canal towards surface; *ch*, chromatophore; *co*, cortex; *cu*, cuticle; *e*, secretory cells; *f*, fucosan-receptacle; *m*, meristoderm; *s*, secretory spaces and canals.

although they have the characteristics of secretory cells, they do not produce a connected epithelial layer. Oliver ((121) p. 100) describes the formation of tylose-like structures from these cells.

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According to Guignard the secretory cells develop secondarily in *Laminaria*. In *Macrocystis*, however, Skottsberg ((179) p. 129) recognises them before the appearance of the mucilage-space, although, since the secretory cells do not keep pace with the radial elongation of the latter, they are subsequently found mainly at its inner margin. In the young lamina of *Nereocystis* the secretory cells form a complete investment to the canal ((105) p. 290). The mucilage within the canals of *Laminaria* differs from that of the cell-membranes ((56), (122) p. 165). The large elements recorded by Gain ((45) p. 49) in the medulla of a *Lessonia*, and described as mucilage-canals, are of doubtful nature.

Glands of a different kind occur in *Undaria* (203), as well as in the young plants of certain species of *Laminaria* ((156) pp. 10, 177, 230) and *Alaria*. Those of *Undaria*, which appear as dark dots thickly scattered over both surfaces of the lamina, are single cells of large size (fig. 86 D, F) situated in the hypodermal layer and formed by periclinal division of a surface-cell of the young blade ((204) p. 706). The overlying cell becomes flattened by the rapid enlargement of the gland and ultimately forms a thick hyaline roof to it (fig. 86 F, *r*). In a surface-view the rectangular areas (fig. 86 E) overlying the glandular cells are readily seen. Yendo believed that these cells produced mucilage, but according to Sauvageau ((151), (156) p. 10) they are fucosan-receptacles. The fresh contents are colourless.

(*f*) Origin of Splits and Perforations

As a general rule there would appear to be some factor causing local degeneration of the internal tissues during the development of splits and perforations, a process accompanied by the formation of furrows or depressions on the surface (fig. 87 D), but which of these changes is primary and which is secondary is not always evident from the published accounts. As the depressions gradually deepen with the progressive break-down of the internal tissues, the meristoderm divides and provides a continuous covering (fig. 87 F, G). Ultimately, when the double layer thus formed extends through the whole thickness of the blade, complete rupture occurs, the freshly exposed edges being now entirely overgrown by the meristoderm (fig. 87 G). In most instances at least it seems that there is never more than a very temporary exposure of the inner tissues.

In *Laminaria Cloustoni* ((79) p. 478) the splits are initiated by the appearance of longitudinal furrows which probably result from increased division of the cells of the meristoderm and are often seen sooner on one surface than on the other. As the furrows deepen, breaks appear in the internal tissues and the outer layer ruptures (fig. 87 E), although the exposed edges become rapidly overgrown (fig. 87 F, G). These data are based on a study of regions in front of already established splits, and they imply that, in the species in question, surface-changes are of primary importance, a conclusion apparently reached also by Grabendörfer ((51) p. 660) in *Lessonia*. It is not altogether clear from

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Killian's account whether the internal tissues are actually exposed. He is of the opinion that wave-action plays a considerable rôle in the extension of the splits towards the margin (cf. also (161) p. 206).

In *Macrocystis* ((179) p. 126, (193) p. 805) internal changes are the first to be observed, the inner tissues undergoing gelatinisation which results in the formation of a cavity occupied by mucilage (fig. 87 D, *c*), whilst on either surface active division of the meristoderm causes the formation of furrows.[1] This is in general agreement with the account given by Macmillan ((105) p. 291) for *Nereocystis*; he describes how, as the opposite furrows meet, the separate meristoderm layers unite without any destruction of cells. Wells ((192) p. 223), however, states that it is only the basal perforation that arises in this way, while the forward advance of the splits is due to excessive cortical division which causes rupture of the surface-layer and finally of the whole lamina. This is also stated to be so in *Dictyoneurum*. In *Postelsia*, according to the same authority, the splits arise in regions in which division of the meristoderm is practically at a standstill, so that the lamina here remains thin and gets worn by wave-action; much the same is recorded for *Lessoniopsis*.

Humphrey's account ((69) p. 201) of the development of the perforations in *Agarum* again places stress on a primary growth of the meristoderm. Rapid local multiplication of its cells results in a papillate protrusion on the one surface and of a corresponding depression on the other (fig. 87 A). The meristoderm on this surface penetrates more and more deeply into the underlying tissues and, after reaching the medulla, continues to grow only along the sides of the depression, while that covering its base dies away (fig. 87 B, *1*). The sides thus grow inwards like a circular punch and cut out the part of the medulla still remaining in the centre of the perforation (fig. 87 B, 2). In *A. fimbriatum* Harv. only a few of the papillae become perforated ((134) p. 20).

The diverse observations agree that the edges of the splits are soon covered by rapid growth of the meristoderm and other superficial tissues. In this respect there is a marked contrast to the mode of healing of wounds ((79) p. 468, (109) p. 13, (169) p. 145). If the superficial layers of the lamina or stipe of a *Laminaria* are removed, the intact elements at the exposed surface divide to form perpendicular rows of cells which rapidly cover the wound. In his studies of regeneration in Laminariales Setchell ((169) p. 145) found that it is always the inner cortex and medulla that grow out to form the new organs.

The same authority ((163) p. 45, (169)) has drawn attention to certain special features connected with blade-renewal in the species of *Laminaria*. In *L. Sinclairii* the first sign of the inception of this process is the appearance of a slight dilation (fig. 65 J, *c*) in the transition zone. This is followed (fig. 65 K) by a transverse rupture at this level and the rapid separation of the two edges (fig. 65 E, L, M) as the new blade (*nb*) develops from the more internal tissues; the ruptured surface layers form collars (*c*) at the top of the stipe and at the base of the old blade. Blade-renewal is thus effected solely by inner cortex and medulla; the

[1] The contrary account of Rosenthal ((138) p. 123) is described as erroneous by Skottsberg.

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outermost elements of the former divide actively at right angles to the surface and give rise to a new meristoderm by the division of which a new outer cortex is formed. Dr Lund (cf. p. 226) has observed similar

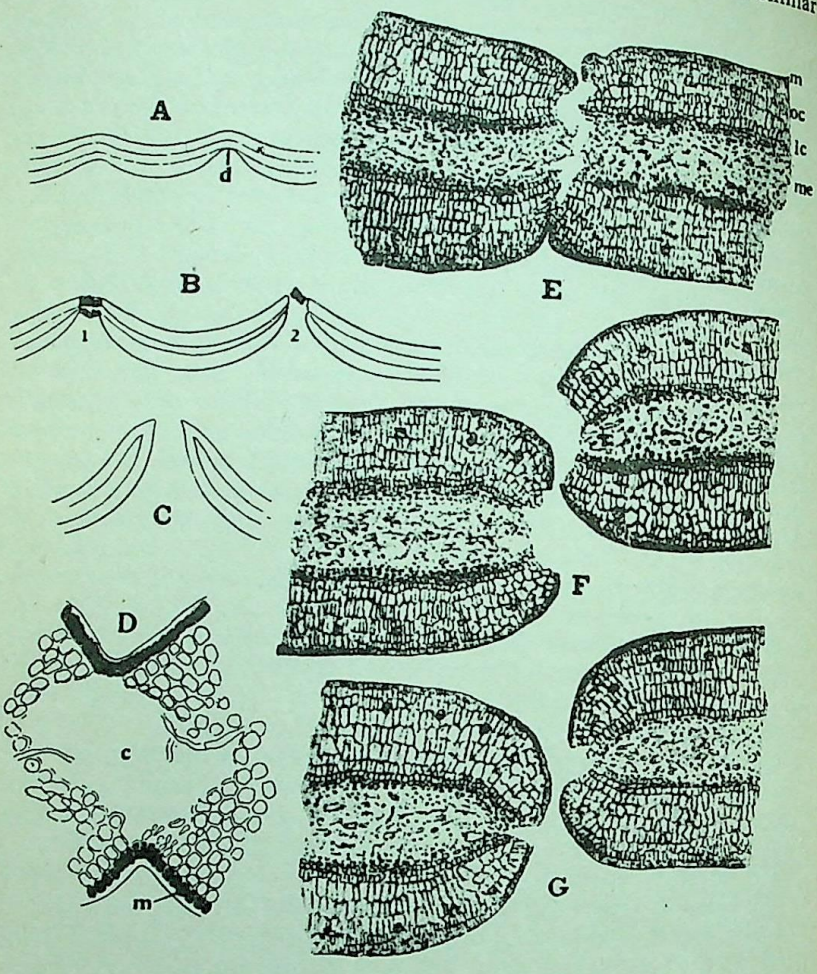

Fig. 87. A–C, *Agarum cribrosum* (Mert.) Bory, successive stages in formation of the perforations (after Humphrey). D, *Macrocystis pyrifera* (Turn.) Ag., transverse section of blade showing early stage in split-formation (after Skottsberg). E–G, *Laminaria Cloustoni* Edmonds., successive stages in healing of the edges of a split in the blade (after Killian). *c*, cavity; *d*, depression; *ic*, inner cortex; *m*, meristoderm; *me*, medulla; *oc*, outer cortex.

events in *L. Cloustoni*, but it is not known whether comparable changes are met with in other Laminariales exhibiting blade-renewal. The shifting of meristematic activity to deeper layers is paralleled in the older stipe by the secondary growth which is initiated in the outer cortex (p. 232).

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(*g*) Air-bladders

The walls of the air-bladders of *Nereocystis* (105) and *Macrocystis* ((179) p. 125) consist for the most part of cortex, although the inner part contains some sieve-tubes; in *Macrocystis* numerous hyphae project into the cavity. According to Macmillan a second meristematic zone is distinguishable in the inner part of the wall of the bladder of *Nereocystis*.

The bladders of *Nereocystis* have a capacity of several litres. The contained gas is stated to include carbon monoxide (1–12%), which is formed only in the presence of oxygen and is believed to be a product of respiration (98, 99, 137, 211); Zeller and Neikirk (207), however, record only carbon dioxide in considerably larger quantities than in atmospheric air. The pressure within the bladder is often less than that of the atmosphere and varies at different times of the day (40, 211); nevertheless the bladders can resist considerable external pressure without collapsing (70).

(*h*) The Haptera

The succession of rhizoids that serves to attach the young plants (fig. 81 H) is later replaced by the broadened base of the enlarging stipe, which forms a disc fastened by numerous rhizoids and showing no appreciable internal differentiation ((79) p. 463), although the inner cells are somewhat elongated. In older plants the disc is mostly replaced by special haptera which are arranged in approximate whorls and arise in succession from progressively higher levels on the stipe (figs. 65 N; 66 I). They first appear as slight superficial puckerings and in *Laminaria Cloustoni* ((79) p. 465) are formed at the time of most active growth, soon after the appearance of the new blade. The later ones often show considerable forked branching.

The haptera are produced by tangential division of the outermost cells of the stipe ((195) p. 23), although Church ((22) p. 63) states that the older ones arise endogenously. Cell-division is localised in the apical region ((79) p. 464, (132) p. 374, (161) p. 199, (179) p. 93), where the cells are often arranged in well-defined rows. The inner part of the mature hapteron consists of elongate mechanical cells (cf. also (105), (158), (181) p. 580), with strongly thickened transverse walls which are often provided with numerous pits ((31), (79) p. 464). There is no medulla, although a few hyphae may be present; mucilage-canals are sometimes found. When the substratum is reached, the tip of the hapteron spreads out and the surface-cells grow out into densely packed rhizoids ((79) p. 465, (161) p. 199). Growth in length may continue after attachment, so that the primary disc is lifted off the substratum ((185) p. 399). In *Pterygophora* Macmillan ((107) p. 732) describes growth-rings in the older haptera.

More specialised attaching organs are found in *Saccorhiza* and *Macrocystis*. In *S. bulbosa* most of the haptera arise from the bell

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(p. 201) and this is also so in *S. dermatodea*, where the latter is far less conspicuous. The development of the bell ((10), (156) p. 104, (161) pp. 183, 198) is largely due to expansion of the medulla, the cortex playing only a passive rôle. In *Macrocystis pyrifera* Skottsberg ((179) p. 93) distinguishes, apart from the ordinary haptera which become attached at their tips, others that curl round foreign objects and so help in fixation. The attaching organs of the Californian forms of *Macrocystis* have been fully studied by Setchell (174); those of *M. integrifolia*, in particular, are very elaborate, being prostrate and developing numerous floating shoots from their margins.

ASEXUAL REPRODUCTION

The extensive sori (fig. 88 A, *s*), the position of which in the different genera has already been described, invariably comprise only unilocular sporangia[1] intermingled with abundant unicellular paraphyses. Their development[2] takes place in essentially the same way in all Laminariales. The superficial cells grow out as a palisade-like layer (fig. 88 B), and each protuberance sooner or later divides tangentially into a small basal cell (*b*) and the future paraphysis (*p*) which continues to lengthen. As the thallus enlarges, the basal cells widen and the paraphyses separate (fig. 88 E); they now occupy only part of the surface of the basal cell (fig. 81, K, *p*). The apices of the paraphyses, however, usually broaden and remain in close contact with one another. During the outgrowth of the paraphyses the mucilaginous cuticle of the superficial cells is often merely stretched (fig. 88 B, *cu*) and constitutes a protective covering to the developing sorus; in *Saccorhiza bulbosa* ((156) p. 42) this layer even undergoes further thickening (fig. 88 C, *cu*).

The paraphyses (fig. 81 K, *p*), which are usually club-shaped, show a more or less marked gelatinous thickening of the membrane at their expanded outer ends. Here lie numerous chromatophores (*ch*), whilst there are often abundant fucosan-vesicles in the interior. The oblong sporangia arise from the basal cells between the paraphyses (figs. 81 J; 88 C, E, *sp*) and are thus protected during development. The efficiency of the paraphyses, however, no doubt varies. In *Laminaria* and other genera the thick outer membranes often flow together to form a continuous covering over considerable areas. On the other hand, in *Saccorhiza dermatodea* ((161) p. 207) and in *Cymathere* ((53) p. 92) the paraphyses have only a slightly thickened tip.

The number of zoospores produced in the sporangia seems to vary. 32 are recorded in *Laminaria* ((159) p. 344), *Alaria esculenta* ((156) p. 224), *Pterygophora* ((104) p. 122), and *Eisenia* ((23) p. 496, (67) p. 37),

[1] The plurilocular sporangia recorded by Buffham (19) belong to *Streblonema aequale* (p. 58).

[2] See (23), (67) p. 35, (93) p. 35, (156) p. 42, (158) p. 162, (161) p. 207, (190) p. 240.

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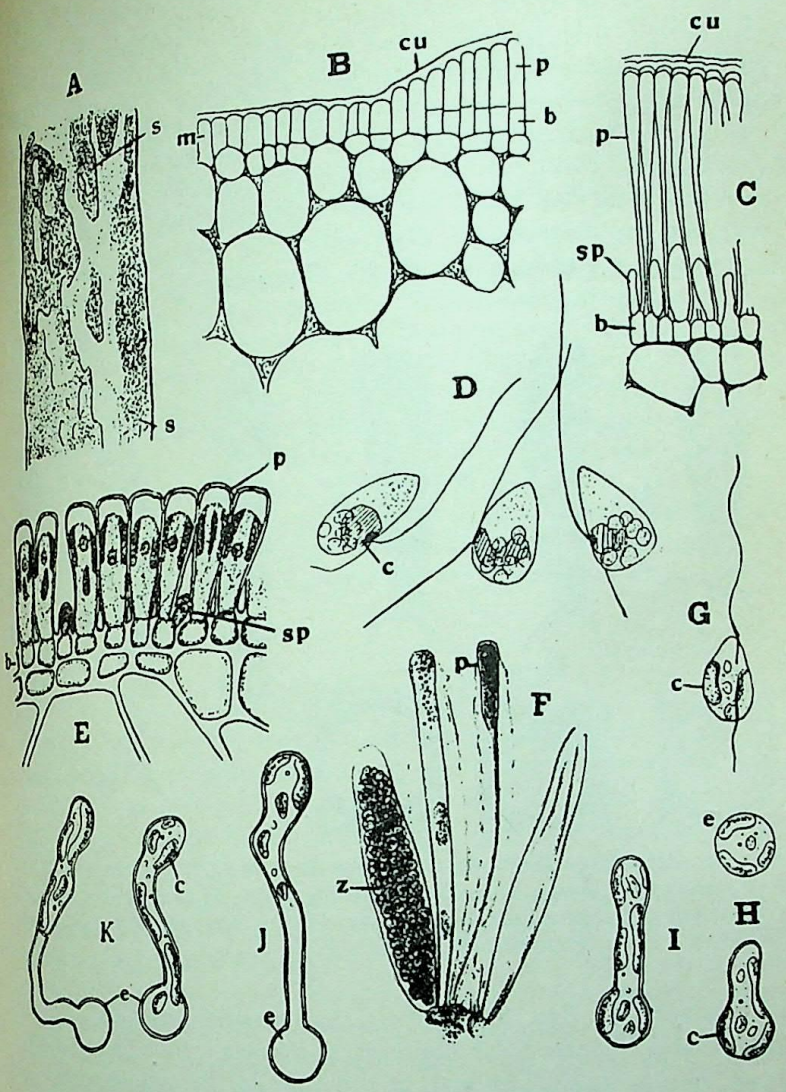

Fig. 88. Asexual reproduction of Laminariales. A, *Laminaria digitata* (L.) Lamour., small part of a frond with sorus (*s*). B–D, F, *Saccorhiza bulbosa* De la Pyl.; B, early and C, later stage in development of a sorus; D, zoospores; F, two sporangia (one dehisced) with two paraphyses. E, *Chorda filum* (L.) Lamour., young sorus in transverse section. G–K, *Costaria costata* (Turn.) Saund.; G, zoospore; H, embryospore and first stage in germination; I–K, later stages. *b*, basal layer of sorus; *c*, chromatophore; *cu*, cuticle; *e*, embryospore; *m*, meristoderm; *p*, paraphysis; *sp*, sporangium; *z*, zoospores. (A–D after Sauvageau; E after Kylin; G–K after Kanda; F after Thuret.)

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sometimes 64 in the last two. On the other hand, in *Chorda* (fig. 81 K; (93) p. 36) there are 16, while in *Saccorhiza bulbosa* (fig. 88 F) 128 is given as the probable number ((156) p. 44). Zoospore-development commences with successive nuclear division (fig. 89 A–D), accompanied by multiplication of the chromatophores (*c*), and takes place in essentially the same way as in Ectocarpales (p. 118). Thus, in *Chorda* ((93) p. 36) the 16 nuclei (fig. 89 E, *n*) at first lie in the middle of the sporangium, while the 16 chromatophores (*c*) occupy a peripheral position; later the nuclei migrate outwards and become associated with the chromatophores, after which the rudiments are cut out by simultaneous cleavage (fig. 89 F). The sporangia of a sorus develop

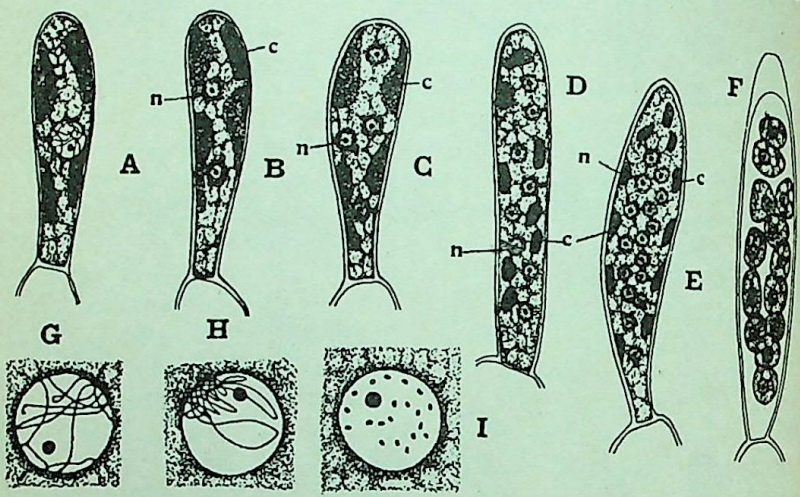

Fig. 89. Zoospore-development in *Chorda filum* (L.) Lamour. (after Kylin). A–E, successive stages in nuclear multiplication; F, formation of zoospores; G, nucleus of sporangium in prophase; H, the same, synezesis; I, the same, diakinesis. *c*, chromatophore; *n*, nucleus.

successively (cf. figs. 81 K; 87 C), although considerable numbers mature and liberate their contents at the same time ((67) p. 37, (156) p. 44, (159) p. 344). The wall at the apex of the mature sporangium usually becomes strongly thickened (figs. 88 F; 89 F; (65) p. 346, (93) p. 37, (104) p. 123, (156) p. 44), and dehiscence occurs here (cf. fig. 88 F). Sauvageau suggests that it is aided by the pressure of the gelatinous paraphyses on the sporangia. The whole contents, enveloped by a delicate membrane, are liberated with a jerk and gradually emerge from between the paraphyses.

The zoospores are of the usual type (fig. 88 D) and generally possess a single plate-shaped chromatophore which often occupies a considerable part of the periphery ((76), (104) p. 123); in *Chorda* there are a number of chromatophores. The swarmers commonly tend to

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move away from strong light (cf. however (213) p. 17), but the presence of an eye-spot is variable.[1]

Kylin ((93) p. 35) showed in 1918 that the first nuclear divisions in the sporangium of *Chorda* are meiotic (fig. 89 G–I), and this has since been proved by McKay ((104) p. 120) for *Pterygophora* and by Hollenberg ((67) p. 35) for *Eisenia* (cf. also (115)). The haploid chromosome-number is given as 13–15 (20 in *Chorda*). There can be no doubt that all Laminariales normally show an alternation of cytological phases.

As a rule the sori differentiate only on mature parts, which have practically completed their growth. Their development usually coincides with the commencement of the cold season, and the fertile parts often persist through a considerable part of the winter. Precise data, which are rarely available, indicate some degree of variability. Harries ((58) p. 894) showed that the three species of *Laminaria* (*digitata*, *saccharina*, *Cloustoni*), found on the Welsh coast, mature in the order named, and concludes that this is correlated with their position on the shore (cf. also (30) p. 179), whilst Sauvageau ((156) pp. 137, 201) reports finding sori on adult plants of *L. digitata* and *L. saccharina* at all times of the year. The sori are commonly devoured by Mollusca ((156) p. 12).

THE GAMETOPHYTES

Although the female prothalli are often more or less clearly pictured in some of the older figures depicting the development of the young plants,[2] it was only in 1915 that Sauvageau (148, 149) reported the existence of heteromorphic alternation with two sexes of gametophytes. Prior to that it was generally held that the Laminariales showed no sexual reproduction; erroneous observations of Drew (30), on the sexuality of the swarmers produced by the sporophyte, were disproved by Lloyd Williams (197). In 1916 Sauvageau (152) followed up his first discovery by the description of the gametophytes of *Laminaria digitata* and *L. saccharina* and later (150) of those of *Alaria esculenta* (see also (124)). In the same year Kylin (92) confirmed Sauvageau's observations on *L. digitata* (cf. also (90)) and in 1918 (93) described the gametophytes of *Chorda*. It was not, however, until 1921 that Williams (198) observed the spermatozoids and the process

[1] Thus, Sauvageau (156) found none in *Laminaria* (cf. also (76) p. 255), but records one in *Chorda* (cf. also (77) p. 105, (110)), *Saccorhiza*, and *Alaria esculenta*; on the other hand, Kuckuck ((89) pl. 8, fig. 8) shows an eye-spot in *Laminaria* (cf. also (71)), while Printz ((128) p. 16) failed to observe it in *Alaria*. It is also recorded in the zoospores of *Egregia* ((115) p. 228), *Pterygophora* ((104) p. 123), and *Eisenia* ((67) p. 37). The recent statements that flagella are lacking in *Pelagophycus* and *Eisenia* are erroneous ((67) p. 37).

[2] See (7), (30), (79), (196), (197). Williams (196) in 1900 described the formation of branched filaments from germinating zoospores.

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of fertilisation. Since then the gametophytes of numerous Laminariales have been described.[1]

The swarmers of a sporangium give rise partly to male and partly to female gametophytes. This was established by Sauvageau (149), who in *Saccorhiza bulbosa* observed the germination of the spores into the two kinds of prothalli while still enclosed within the sporangium; a similar observation was later made on *Laminaria Cloustoni* ((156) p. 192). By allowing the sporangia of a sorus of *Laminaria* to liberate their contents into solidifying gelatine, Schreiber (159) isolated the individual groups of spores and by subsequent culture showed that male and female gametophytes are produced in equal numbers from a sporangium. Sex determination in this genus, and probably in all Laminariales, is therefore genotypic (cf. also (156) p. 4). The occurrence of swarmers of two sizes has occasionally been recorded (29, 156), but such differences appear neither to be constant (cf. (103), (213) p. 22), nor to be related to sexual differentiation.

The early stages of germination of the two kinds of zoospores are identical ((92) p. 554, (93) p. 21) and the differences between the sexes usually become apparent only after some time, although in *Chorda* ((94) p. 70, (198)) they are evident before the gametophytes are a week old (cf. also (156) p. 45). The swarmer rounds off and secretes a thin membrane (fig. 88 H); the resulting embryospore puts out a slender outgrowth into which the bulk of the contents pass (fig. 88 H–J). Gradually the distal extremity of the tube becomes dilated (fig. 88 J, K) and at this stage the germling often appears dumbbell-shaped. Finally the contents collect within the swelling, which becomes separated by a septum (fig. 88 K), the orientation of which is independent of the direction of the incident light. It is this cell that divides to form the actual gametophyte and, even in late stages, the empty spore-membrane with its tubular outgrowth may remain attached to the prothallus (cf. fig. 90 D, F, I, *e*). In *Alaria esculenta* ((156) p. 227), where the spore occasionally retains part of its contents, it may subsequently give rise to a second gametophyte, but this is exceptional.

The filamentous gametophytes are commonly well branched and possess rather elongate cells containing a number of approximately discoid chromatophores; their habit is heterotrichous and growth is usually slow. The natural substrata are probably rocks and other Algae ((92) p. 560). The male gametophytes (fig. 90 F, L) are nearly always more copiously branched than the female, although the reverse condition has been reported in *Costaria* ((3); cf. however (76) p. 239). On the other hand, the cells of the male gametophyte, though usually more numerous, are invariably smaller than those of the female and sometimes also paler in colour ((58) p. 899, (59) p. 217). In *Chorda* ((77) p. 105, (93), (198)) the gametophytes are exceptionally robust and

[1] See the enumerations in (70*a*) p. 212 and (23), (65), (67), (114), (209) and (213).

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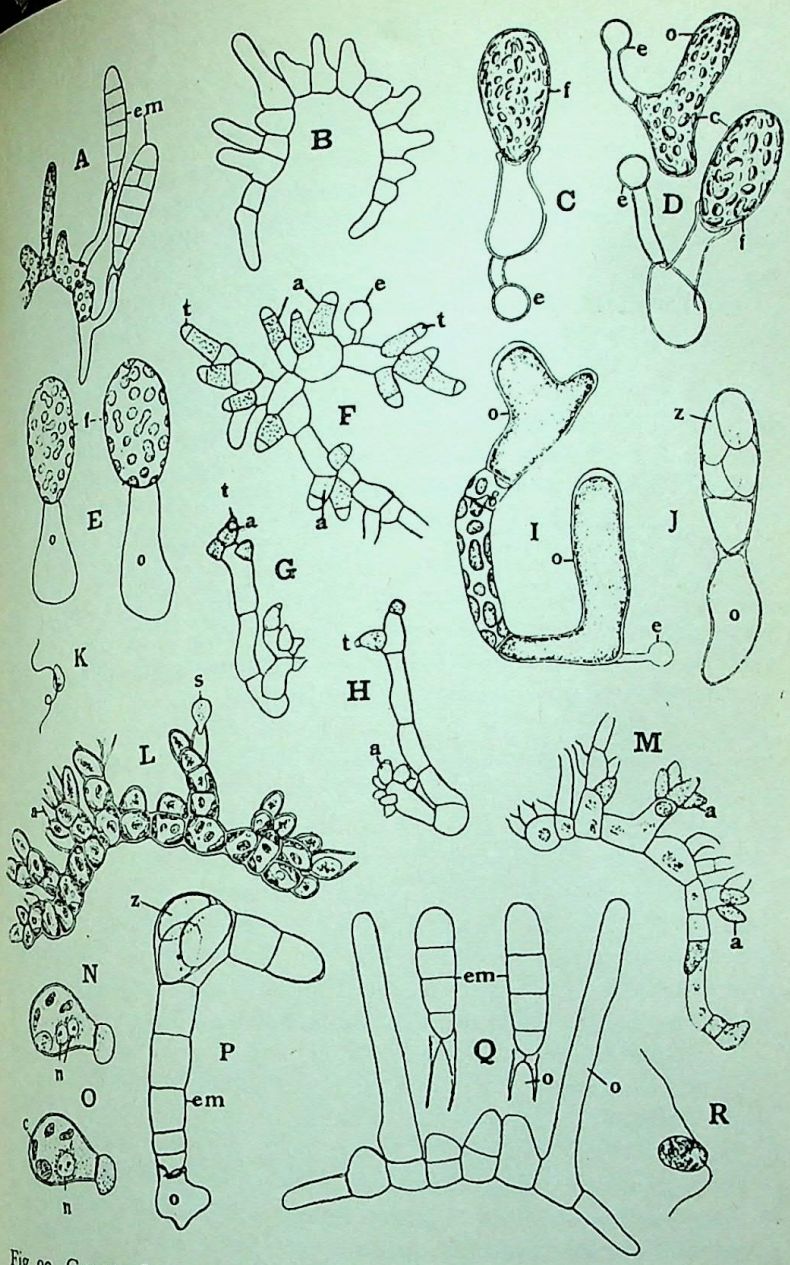

Fig. 90. Gametophytes of Laminariales. A, B, F, Q, *Laminaria digitata* (L.) Lamour.; A, B, Q, female gametophytes, in A with two embryos (shown separately in Q); F, male gametophyte. C, D, *Arthrothamnus bifidus* (Gmel.) J. Ag., female gametophytes. E, G, H, *Saccorhiza bulbosa* De la Pyl.; E, female and G, H, male gametophytes. I, M, *Alaria esculenta* (L.) Grev.; I, female and M, male gametophytes. J, P, *Laminaria saccharina* (L.) Lamour., embryos showing zoospore-formation. K, L, *Alaria crassifolia* Kjellm.; K, spermatozoid; L, male prothallus. N, O, R, *Macrocystis pyrifera* (Turn.) Ag.; N, O, fertilisation; R, spermatozoid. *a*, antheridium; *c*, chromatophore; *e*, embryospore; *em*, embryo; *f*, ovum; *n*, nucleus; *o*, oogonium; *s*, spermatozoid; *t*, thickening of antheridial wall; *z*, zoospores. (C, D, K, L after Kanda; I, M after Printz; J, P after Pascher; N, O, R after Levyns; the rest after Sauvageau.)

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richly branched, while in *Egregia* according to Myers ((115) p. 229) both kinds consist of only a few cells.[1]

The data on the size of the gametophytes are, however, based on observations made in cultures, where their development is likely to be retarded (cf. (20), (110)). Both form and size do in fact vary appreciably with the temperature, the light-intensity, and the kind of nutrient salts available ((58), (76) p. 256, (92) p. 557). According to Schreiber ((159) p. 336) gametophytes, as well as sporophytes, of *Laminaria* exhibit good growth even at higher temperatures, although they remain sterile (cf. also (191)); when the temperature is lowered gametes are produced (cf. however (67) p. 38), whilst when it is raised their formation is arrested. This perhaps accounts for the practical restriction of Laminariales to colder seas. Regeneration of the gametophytes from fragments or isolated cells has been reported ((59) p. 214, (159) p. 335).

The *antheridia*[2] (fig. 90 F–H, L, M, *a*) arise singly or in groups at the tips of the erect threads or as lateral outgrowths from the upper side of the creeping threads; intercalary antheridia, formed by transverse division of the cells, are not uncommon. The antheridia are small, colourless or almost colourless structures, which at best contain only one or two much reduced chromatophores ((67) p. 39, (92) p. 553, (93) p. 22, (94) p. 71, (156) p. 146). The entire contents are utilised to form a single spermatozoid. The wall at the apex becomes protruded and markedly swollen (fig. 90 F, G; (67) p. 38, (198) p. 605), and here an aperture is formed (fig. 90 L) through which the male cell (*s*) is liberated. The ellipsoidal or pyriform spermatozoids ((76) p. 256, (104) p. 126), about 4 μ long, possess the usual two laterally attached flagella (fig. 90 K, R); an eye-spot is reported in *Pterygophora* (104), but appears usually to be lacking. The male gametophytes commonly die after liberation of the sperms. Sauvageau ((156) p. 3) comments on the marked protandry exhibited by the species studied by him.

In the female prothalli (fig. 90 I, Q) any or all of the cells may enlarge to form oogonia (*o*). The latter are either pear-shaped with the upper extremity narrowed or dilated, or they may be tubular (fig. 90 D, I) or even lobed ((128), (156) p. 227). The wall at the distal end of the oogonium usually becomes greatly thickened ((156) p. 51) and in *Laminaria* (198) three distinct layers can be distinguished. The numerous chromatophores become crowded together at the apex of the mature organ with their long axes parallel to it, which probably indicates a marked internal pressure playing a rôle in dehiscence. The

[1] In *Pleurophycus* (4), as well as in *Costaria* and *Arthrothamnus* (76), prothalli that differ in minor particulars from the ordinary type have been described.

[2] In *Laminaria religiosa* Ikari (71) recorded two kinds of male gametophytes bearing unilocular and plurilocular organs respectively. There can be no doubt, however, that those with plurilocular sporangia belonged to some foreign alga (Ectocarpales?) that had invaded his cultures ((76) p. 255). Ikari's figure of a monoecious gametophyte is probably an error of observation, since zoospores often germinate in close juxtaposition (cf. also (87) p. 174).

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entire contents form a single ovum, which is normally liberated prior to fertilisation through a narrow apical aperture (fig. 90 C). After the female cell has emerged, the thick elastic edges of the wall again meet and form a platform to which the ovum usually remains attached for some considerable time after fertilisation (fig. 90 C, Q). In *Chorda* ((94) p. 72, (198) p. 606) the mature ovum merely lengthens out of the oogonium, whilst in *Macrocystis* (fig. 90 N, O) it is stated to be retained until after fertilisation ((103) p. 351, (191)); this is not confirmed by Papenfuss ((213) p. 22).

Nuclear fusion has been observed in *Laminaria* (198), *Pterygophora* ((104) p. 128), *Macrocystis* ((103) p. 351), and *Eisenia* ((67) p. 40). In *Pterygophora* the fusion nuclei are in early prophase, while in *Eisenia* both gametes are stated to enlarge appreciably during fusion. The zygote secretes a thin membrane and develops into the sporophyte without any resting period. Parthenogenesis has been reported by Schreiber ((159) p. 341), but its occurrence in nature is not established; the germlings from the parthenogenetic ova show irregularities in division. The possibility for natural hybridisation must be considerable, but Schreiber's attempts to produce hybrids artificially were unsuccessful.

In *Saccorhiza bulbosa* ((156) p. 51) the female zoospore commonly gives rise directly to an oogonium (fig. 90 E), without any vegetative phase. This is the simplest type of gametophyte known among Brown Algae, and its discovery has played a considerable rôle in the interpretation of the life-cycle of Fucales (p. 380). Such extreme reduction seems to be frequent in this species, although occasionally much more extensive gametophytes are formed ((156) p. 51). A tendency to reduce the female gametophyte to a single cell has been observed in cultures in other Laminariales; thus, it has been reported in *Laminaria* ((156) p. 146, (198)), *Egregia* ((115) p. 229), *Macrocystis* ((103) p. 350), and *Arthrothamnus* (fig. 90 C; (76) p. 234). The one-celled condition seems to be frequent in *Laminaria Cloustoni* ((156) p. 193) and in *Arthrothamnus*, but it remains to be determined how far such simple prothalli are the result of cultural conditions. According to Sauvageau (155) the female prothalli of *Phyllaria reniformis* Rostaf. are "parasitic" in *Lithothamnion lichenoides*.

THE STATUS OF THE LAMINARIALES

In cultures of *Laminaria saccharina* Pascher (123) reports a precocious development of sporangia in embryos in which surface-development was just beginning. Other embryos, still in the filamentous (2–8-celled) stage, produced 4–8 swarmers from certain of their cells (fig. 90 J, P, *z*), and instances were even observed in which the fertilised ovum, without further segmentation, divided to form a number of reproductive elements. The last condition does not differ

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from that which obtains in an isogamous or oogamous Green Alga. These observations suggest that, under certain circumstances, production of zoospores might take place without the development of an elaborate sporophyte, and they lend support to the view of an ultimate isomorphic origin for the sharply distinct generations of Laminariales.

Moreover, both they and the early stages of development of the sporophyte point to simple filamentous ectocarpoid types for the derivation of these elaborate forms. It is noteworthy that, while the gametophytes are heterotrichous and in great part prostrate, the sporophytes, even in the reduced stages just described, are erect from the first. The Laminariales may in fact be regarded as exhibiting to an extreme the elaboration of the sporophyte so evident among Ectocarpales, while the filamentous heterotrichous habit has been retained by the gametophyte (cf. also (212)). The absence of a prostrate system in the sporophyte finds its parallel in other highly differentiated series (cf. pp. 179, 191).

The Laminariales would thus exhibit the ultimate development of the tendency towards a parenchymatous construction evident among Ectocarpales and realised in such forms as *Litosiphon* and *Stictyosiphon*. The relatively simple genus *Chorda* is relevant in this connection, for although it is quite like other Laminariales in reproduction and life-history, it is less specialised morphologically and anatomically. It may well owe its simplicity to the non-differentiation of an expanded lamina, since this probably necessitates a more elaborate mechanical construction, such as is supplied by the medulla of the stipe of most Laminariales. The marked activity of the meristoderm is foreshadowed in diverse parenchymatous Ectocarpales (p. 114). The specialised sori of Laminariales are likewise already indicated in some of the more advanced representatives of the latter order.

Both Laminariales and Fucales show the development of a far more elaborate plant-body than is usually found among Algae. Alike in their morphology and their anatomy they exhibit features, which find a certain degree of parallel among higher land-plants (22) and are probably an expression of general tendencies in somatic evolution. Since the early stages in the origin of land-plants are likely to remain unknown, these elaborate Brown Algae may perhaps afford some data as to the possible lines of development that were followed. It must be emphasised, however, that the system of intergrading tissues met with in these forms is without parallel among higher plants.

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CLASSIFICATION AND GEOGRAPHICAL DISTRIBUTION

The classification—largely based on Setchell ((162) p. 337, (176) p. 590) —that has been adopted in the preceding matter is as follows:

1. *Chordaceae:* Chorda.
2. *Laminariaceae:*
   (*a*) *Laminarieae:* Laminaria, Phyllaria, Saccorhiza.
   (*b*) *Cymathereae:* Cymathere, Pleurophycus.
   (*c*) *Agareae:* Agarum, Costaria, Thalassiophyllum.
   (*d*) *Hedophylleae:* Arthrothamnus, Hedophyllum.
3. *Lessoniaceae:*
   (*a*) *Lessonieae:* Dictyoneuropsis, Dictyoneurum, Lessonia, Nereocystis, Postelsia.
   (*b*) *Macrocysteae:* Macrocystis, Pelagophycus.
   (*c*) *Lessoniopseae:* Lessoniopsis.
4. *Alariaceae:*
   (*a*) *Alarieae:* Alaria, Hirome, Phyllogigas(?), Pterygophora, Undaria.
   (*b*) *Ecklonieae:* Ecklonia, Eisenia.
   (*c*) *Egregieae:* Egregia.

The Laminariales are characteristic of colder seas, and their chief centres of distribution (see the map) are circumpolar in the Arctic and Antarctic regions (162). Here they occur wherever there are suitable substrata, free from permanent ice ((140) p. 150). From the polar regions they extend into the temperate zones and, where cold ocean currents sweep along the coasts, as for instance along the shores of Lower California and Peru ((68) pp. 2, 55) or the west coast of South Africa, certain genera penetrate far into subtropical or even tropical regions. The genera occurring in the Northern and Southern Hemispheres are in large part distinct.

Typical of the Northern Hemisphere are the Chordaceae, Laminarieae, Alarieae, and Agareae, although the last-named are restricted to North America, Greenland ((2) p. 18, (63), (75) p. 24, (140) p. 169), and adjacent parts of Asia (cf. (69) p. 198 and the map, *Ag*). The *Laminarias* are essentially northern in their distribution (13, 81), although *L. Lejolisii* flourishes on parts of the Atlantic coast of Morocco (26) and a few species are frequent in the Southern Hemisphere (e.g. *L. pallida* (Grev.) J. Ag. at the Cape (25), (213)). *Saccorhiza dermatodea* and *Alaria Pylaii* (Bory) J. Ag. occur over a large area of the North Atlantic ((38) p. 74, (49) p. 75, (75) pp. 21, 31, (84) p. 20, (140) p. 169). South of the Cape Cod Peninsula Laminariales only play a small rôle ((34) p. 5) on the eastern shores of North America. In the Mediterranean *Phyllaria reniformis* (Lamour.) Rostaf., *Saccorhiza bulbosa* ((5) p. 144, (157) p. 4), and *Laminaria Rodriguezii* have alone been recorded; the last is stated

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to occur mainly at depths of 100–150 metres (17). Berthold (11) lists no member of the order from the Gulf of Naples.

The Pacific shows a considerably greater diversity of forms than does the Atlantic, and both on the Asiatic and on the American shores ((175) p. 168) members of the order extend far towards the south, although the two floras are in part distinct. Characteristic of the North Pacific, both on the American and Asiatic shores, are the Cymathereae (44), (82), (146) p. 393), *Thalassiophyllum*, the Hedophylleae (*Hedophyllum*, *Arthrothamnus*), and *Costaria*. *Undaria* (see map 2, *U*) appears to be confined to Asia, while along the American shores and in part extending down to Lower California are found a number of characteristic Lessonieae (*Dictyoneurum*, *Postelsia*), as well as the genera *Costaria*, *Pelagophycus*, *Nereocystis* (cf. also (112) p. 72), *Lessoniopsis*, *Pterygophora*, *Eisenia*, and *Egregia* (see map 2); of these *Pelagophycus* is restricted to the southern part of this region. As compared with the Arctic regions the Californian coast has fewer Alarieae and is much poorer in Laminarieae (here *L. Sinclairii*) and Agareae (only *Costaria*).

The characteristic Laminariales of the Southern Hemisphere are *Lessonia*, *Ecklonia*, and *Macrocystis* ((60) p. 457, (61) p. 217), while the imperfectly known genera *Phaeoglossum* and *Phyllogigas* are at present only recorded from the Antarctic (179). *Macrocystis* (see map 2) is probably most abundant on the shores of Patagonia ((179) p. 132), extending from here down to the area of permanent ice, but it is also widespread in Australia and New Zealand, and South Africa; in the last-named area it is practically confined to the east coast with its colder water ((27) p. 63). *Ecklonias* are well represented in Australia, as well as in South Africa, which harbours the largest species of the genus (*E. buccinalis*). Most of the striking *Lessonias* are confined to the South American region around Cape Horn, although *L. flavicans* is recorded from New Zealand. *L. laminarioides* is a characteristic component of the flora of Japan and of the adjacent shores of Siberia.

Macrocystis pyrifera (see map 2) has the widest distribution of all species of Laminariales. Its area extends over the whole of the Southern Subantarctic zone ((60) p. 461) whence it has been distributed by Antarctic currents to many of the outlying islands (Kerguelen, Tristan d'Acunha, St Paul Island). It follows the Humboldt current up the western shores of South America (here accompanied by *Eisenia Cokeri* and *Lessonia nigrescens*) as far as the equator (68), and, passing to the cold waters flowing in from the North Pacific, extends along the entire western coast of North America up to British Columbia ((162) p. 365, (174) p. 446).

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Order VII. *SPHACELARIALES*

The five orders considered in the preceding pages, all of which exhibit intercalary growth, are no doubt special developments of types of construction represented among Ectocarpales, although the members of the latter order do not attain to the same degree of differentiation or of reproductive specialisation. The three remaining orders of Phaeophyceae are characterised by possessing well-marked apical growth and comprise forms with a parenchymatous construction only; they include no parallel for the pseudo-parenchymatous type exemplified by Cutleriales and Sporochnales. Sphacelariales and Dictyotales also differ in the nature of their life-cycle from the orders previously discussed, since alternation in both is almost certainly isomorphic; in this respect they differ markedly from the polystichous Ectocarpales. The origin of Sphacelariales is probably to be sought among simple filamentous Ectocarpales with isomorphic alternation.

The members of this order are usually copiously branched, although they mostly attain no great size. They afford marked evidence of heterotrichy (figs. 98 A; 99 B) and most are probably perennials, persisting with the help of the prostrate and the basal parts of the erect systems. The diverse branches of the latter are capped by a conspicuous apical cell (fig. 92 C, *a*) cutting off a single row of segments (1–4), which for the most part undergo very regular septation so that the younger parts at least exhibit a definite tier-like structure. The individual branches are nearly always radial in symmetry. The prostrate system (fig. 98) is usually well developed and in the more specialised types commonly takes the form of a many-layered crust (fig. 98 G).

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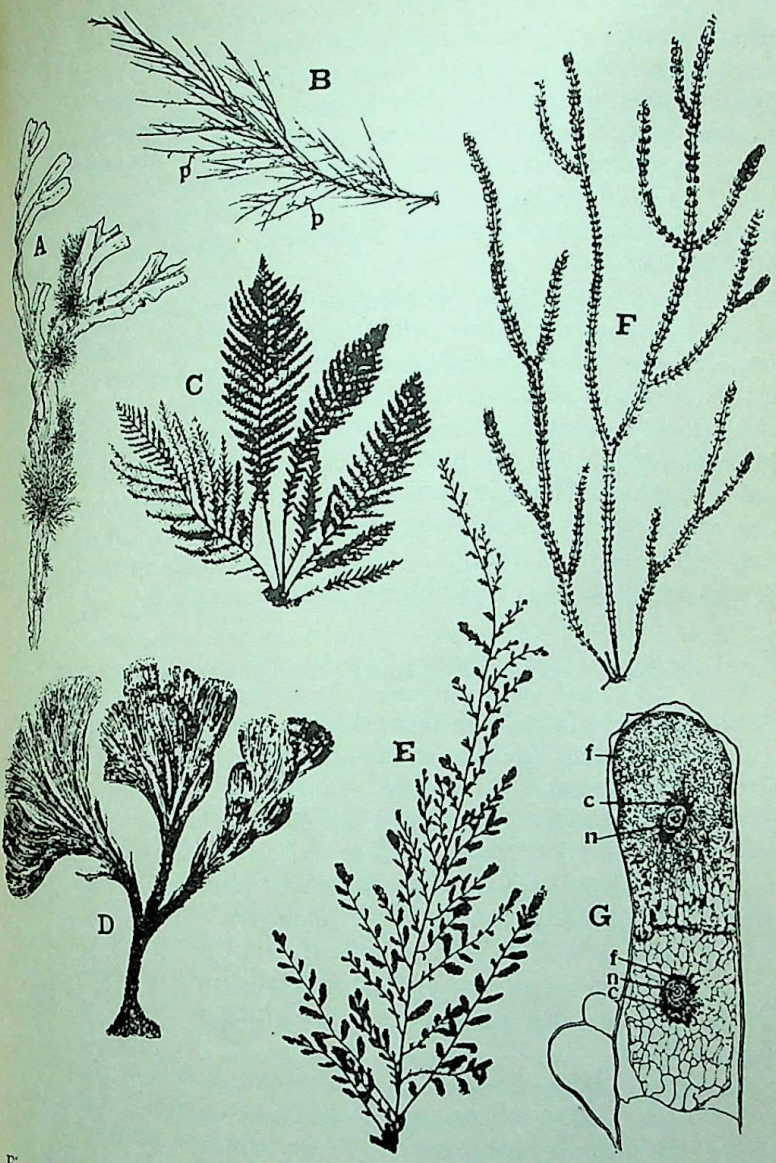

Fig. 91. Habits of Sphacelariales. A, B, *Sphacelaria cirrhosa* C. A. Ag.; A, tufts on *Fucus*, about half natural size; B, single plant bearing propagules (*p*), enlarged. C, *Halopteris filicina* Kütz. D, *H. scoparia* (Kütz.) Sauv. E, *Phloeocaulon foecundum* Sauv., part of a plant. F, *Cladostephus verticillatus* Ag. G, *Halopteris scoparia* (Kütz.) Sauv., apical cell. *c*, centrosome; *f*, fucosan-vesicles; *n*, nucleus; *p*, propagule. (A, B after Taylor; C, F after Newton; D after Kützing; E after Sauvageau; G after Swingle.)

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Hairs, which are invariably provided with a sheath (fig. 95 A), occur in many species.

The cells contain numerous, rather small chromatophores which are lenticular or granular and devoid of pyrenoids. Eau de Javelle causes the cell-walls of all Sphacelariales ((33) p. 2; cf. also (40) p. 215) to assume a black coloration which disappears after some time. The reaction is confined to the older layers of the wall and, when the latter is thin, affects only the middle lamella. According to Sauvageau ((40) p. 216) there is also widespread occurrence of tannin, which is either diffused through all the cells (*Battersia*) or localised in certain peripheral or central elements of the erect system, as in some species of *Sphacelaria*.

In the early part of the century Sauvageau (40-43,46,52) published a series of memoirs dealing with this order; these, which have been largely followed here, considerably amplified and in part corrected the earlier investigations (12,27,31,33). The morphology and anatomy, of the European species at least, are well known, although many details of reproduction and life-history still remain obscure. The few genera are distinguished mainly by the mode of origin of the lateral branches, the behaviour of the segments cut off from the apical cell, and the disposition of the sporangia. Only two of them (*Sphacelaria*, *Halopteris*) comprise any considerable number of species.

HABIT AND GEOGRAPHICAL DISTRIBUTION

Many Sphacelariales form short densely branched tufts, varying from a few millimetres to one or two centimetres in height (fig. 91 A). Several species of *Halopteris* (*H. filicina*, fig. 91 C; *H. scoparia*, fig. 91 D; *H. hordacea*), as well as *Cladostephus* (fig. 91 F), *Phloeocaulon* (fig. 91 E), and *Ptilopogon* ((33) p. 34), attain to larger dimensions, although probably never exceeding about 30 cm. in length; one of the largest of the *Sphacelarias* is *S. plumigera*. In diverse species of *Sphacelaria*, as well as in *Sphacella* (1a,33), the basal system is endophytic and then usually consists of separate threads. Such endophytic forms often exhibit little or no branching of the upright threads (fig. 92 A).

In certain *Sphacelarias* (e.g. *S. olivacea*, *S. radicans*, *S. racemosa*) the few laterals are irregularly arranged and differ in no appreciable respect from the parent axes. As a rule, however, there is differentiation into branches of unlimited and limited growth ((12) p. 480) and very commonly at least the majority of the latter exhibit a distichous arrangement resulting in a pinnate habit (fig. 91 C), although this may become obscured in the older plant by the outgrowth of dormant initials or other irregularities in branching. In the pinnately branched forms the short laterals are either opposite (e.g. *S. plumula*, fig. 92 C; *Chaetopteris*, fig. 101 K) or alternate (species of *Halopteris* and

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Phloeocaulon, fig. 91 E; (12) p. 509). *Cladostephus* (fig. 91 F) is distinguished by the whorled arrangement of these laterals.

The densely tufted, fastigiate habit assumed by *Halopteris scoparia* (*Stypocaulon scoparium* Kütz.)[1] at certain times of the year (fig. 91 D) is, according to Sauvageau ((46) p. 351), due to the abundant outgrowth of dormant branch-initials (cf. p. 279) exhibiting a tetrastichous arrangement, as well as to the sprouting of adventitious branches from the persistent stumps of the short laterals of the previous season. Similar features are no doubt found in other members of the order.

The Sphacelariales commonly inhabit the intertidal region, especially its lower zones, and often penetrate for some distance below low-tide level (*Halopteris scoparia*, *Cladostephus spongiosus*). *Chaetopteris plumosa* is usually found in deeper water, while *Sphacelaria olivacea* may occur in shaded situations near high-water mark (63). Reinke ((34) p. 6) records a free-floating form of *Halopteris scoparia* in the Baltic. In the same region *Sphacelaria cirrhosa* at times assumes an aegagropilous habit (cf. (32) p. 39, (35) p. 65, (54) p. 289, (64)), forming hollow balls reaching the size of a human head. Balls of uncertain origin consisting of numerous plants of *Halopteris funicularis* have been recorded from Tasmania (8).

The Sphacelariales are met with in all seas, although many are inhabitants of temperate and even polar waters ((36) p. 903, (37) p. 99, (58) p. 57). One group of species of *Sphacelaria* is apparently restricted to the Northern (e.g. *S. racemosa*, *S. hystrix*, *S. radicans*) and another to the Southern Hemisphere (e.g. *S. Borneti* Hariot, *S. pulvinata* Harv., *S. divaricata* Mont.). Sauvageau ((43) p. 71, (44)) concludes that the Australasian seas are probably the richest in species of this genus. Some *Sphacelarias* are common to both hemispheres (e.g. *S. cirrhosa* (Roth) Ag., *S. furcigera*), while *S. tribuloides* Menegh. and *S. furcigera* are the species most frequently recorded from warmer seas ((2), (3) p. 81, (7), (61)). In the Mediterranean the genus is poorly represented ((43) p. 71). *Chaetopteris* is mainly confined to the North Atlantic ((11) p. 77, (18) p. 40, (41) p. 144, (62) p. 132).

Halopteris scoparia has been recorded from all parts of the world, while *H. filicina* is widely distributed in the warmer seas of the Northern Hemisphere, although its occurrence south of the equator remains uncertain ((43) p. 421). Most species of *Halopteris* are, however, to be found in the Australasian region, and *H. funicularis* (Kütz.) Sauv. is known from many parts of the Southern Hemisphere. *Phloeocaulon* and *Ptilopogon* are almost confined to Australasia, although *Phloeocaulon squamulosum* Geyler is recorded from South Africa. *Cladostephus verticillatus* seems to enjoy a world-wide distribution, while the occurrence of *C. spongiosus* south of the equator is still doubtful ((52) p. 603). Sauvageau's *Alethocladus* is known only from the Antarctic.

[1] Regarding the difficulty of separating *Stypocaulon* from *Halopteris*, see (43) p. 381.

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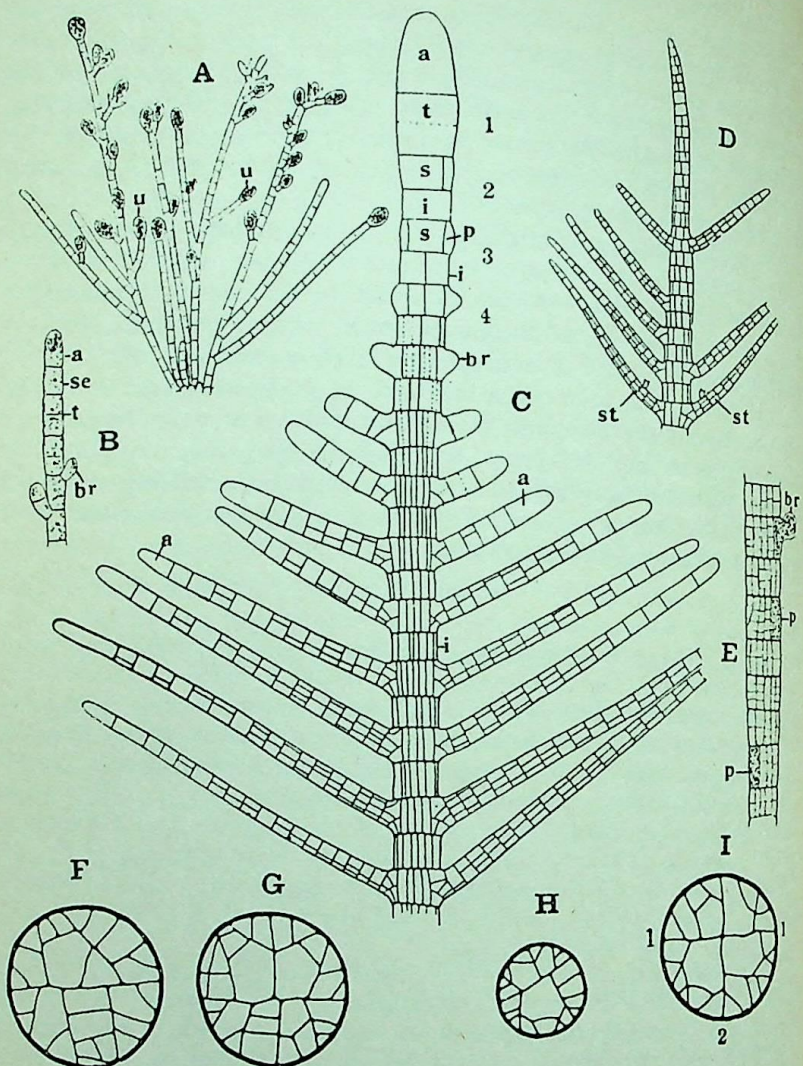

Fig. 92. A, B, *Sphacella subtilissima* Reinke; A, part of a plant with unilocular sporangia; B, part of an erect thread. C, D, F–I, *Sphacelaria plumula* Zanard.; C, apex of a growing thread, 1–4 successive segments of the apical cell; D, apex of a lateral which has completed its growth; F, G, I, transverse sections of inferior segments from older parts of the axis; H, ditto of smaller branch, *1*, *2* the first two walls. E, *S. Reinkei* Sauv., part of a major axis, with branch-initials. *a*, apical cell; *br*, branch; *i*, inferior and *s*, superior secondary segments; *p*, pericyst; *se*, segment; *st*, sterigma of propagule; *t*, septum; *u*, unilocular sporangium. (A, B after Reinke; the rest after Sauvageau.)

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THE ERECT SYSTEM

(*a*) The Apical Cell and its Mode of Segmentation

The prominent elongate apical cells (figs. 92 C; 95 E; 96 A, *a*) commonly contain abundant fucosan-vesicles (fig. 91 G, *f*), as well as a quantity of brown tanniniferous matter which often causes the tips to appear dark brown or black to the naked eye, and it is to this feature that *Sphacelaria* owes its name.[1] This substance is regarded ((43) p. 81) as a reserve, which is utilised during growth; a similar substance commonly occurs in dormant initials and in other parts of the mature plant. The cytoplasm of the apical cells and of the subjacent segments is markedly alveolar (fig. 91 G), while the large nucleus of the apical cell is provided with a centrosome (*c*; (9), (15), (60) and p. 36).

The apical cell cuts off segments parallel to its base (fig. 92 C, *1–4*). When it has reached a certain length, a transverse septum separates a *primary segment* (*1*) from the apical cell proper (*a*). The former again divides transversely (*2*) into two *secondary segments—superior* (*s*) and *inferior* (*i*)—which are usually of equal size,[2] and these divide further (*3, 4*) to produce the mature tissue. In many Sphacelariales (*Sphacelaria*, fig. 92 C; *Chaetopteris*, fig. 101 K; *Halopteris*, fig. 95 H) the secondary segments, though undergoing progressive septation into smaller and smaller cells, exhibit no further evident enlargement. In other words, except in so far as there is production of a special cortical investment in the older parts (cf. p. 268), the diameter of the different branches is essentially that of their apical cell which effects the entire growth in length of the branch ((12) p. 486). These are what Sauvageau ((43) p. 384) calls *leptocaulous* forms.

On the other hand, in the long axes of *Cladostephus* (fig. 96), *Phloeocaulon*, and *Ptilopogon* the secondary segments not only undergo abundant division, but also enlarge more or less appreciably in width and in length. The axis therefore increases in girth from the apex backwards, and the laterals tend to become more widely spaced in the older parts. These are the *auxocaulous* forms of Sauvageau. In *Phloeocaulon foecundum* the primary segments may enlarge to thirty times their original height ((46) p. 441), while in fig. 96 (*Cladostephus*) the tenth segment is already more than three times the length of the first (cf. also (31) p. 147). This is due to continuous elongation of the cells formed by longitudinal division of the secondary segments, a process accompanied by repeated transverse septation. Increase in width is less pronounced, although there may be subsequent broadening as a result of secondary meristematic activity (p. 268). The laterals

[1] σφάκελος = gangrene.

[2] In some *Sphacelarias* (*S. spuria* Sauv. (40) p. 318) the inferior segments are longer than the superior ones, whilst in *S. olivacea* the reverse condition sometimes obtains ((41) p. 55).

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of limited growth, even in the auxocaulous forms, show no enlargement of the segments.

The sequence of division behind the apical cell can often be traced without great difficulty, since the primary septa long remain recognisable (figs. 92 C; 95 E; 96). The two secondary segments soon divide by longitudinal walls. In *Sphacella* ((40) p. 232) and a few species of *Sphacelaria* (*S. pulvinata*, *S. bracteata*) such longitudinal division is quite restricted and may fail to occur in certain segments, but in most Sphacelariales it takes place plentifully so that, at a short distance behind the apex, the diverse branches are multiseriate and consist of a peripheral layer of cells surrounding a central group (fig. 93 D). The central cells commonly develop a slight thickening at the corners, whilst the outer walls of the peripheral cells always become markedly thickened.

In many species of *Sphacelaria* (*S. plumula*, *S. pulvinata*, *S. furcigera*, etc.) the secondary segments divide by longitudinal walls only (fig. 92 C), but in others (*S. radicans* (21) p. 231; *S. olivacea*, *S. racemosa*) transverse septation also takes place sooner or later (fig. 94 A), and this occurs in all other Sphacelariales (*Chaetopteris*, *Halopteris*, etc., fig. 95 E, J) and is especially pronounced in the auxocaulous forms (fig. 96). The secondary segments may form only one series of transverse septa, as usually in *Sphacelaria radicans* and *S. racemosa*, but more commonly there are several series (e.g. *S. olivacea*, *S. plumigera*, *Halopteris*, etc.). Since the transverse septa all arise at about the same horizontal level the tier-like structure is retained.

In *Sphacelaria cirrhosa* and its allies ((42) p. 331) all the longitudinal walls are radial, but in other species their orientation is more varied, and there is probably not the degree of regularity indicated by Geyler ((12) p. 480). Not uncommonly (fig. 92 I) the first two walls (*1*, *2*) are perpendicular to one another and divide the segment into quadrants, whilst the subsequent ones tend to be periclinal and to delimit a superficial layer (fig. 94 F), the cells of which multiply further by anticlinal division (e.g. *S. plumigera* ((41) p. 112, (65) p. 139; *Chaetopteris* (35) pl. 50, (41) p. 145). Quite frequently, however, there are only one or two large central cells surrounded by an irregular peripheral series (fig. 92 F–H), the longitudinal septa having been largely periclinal from the first (e.g. *S. radicans*, *S. plumula* (41) pp. 31, 102).

In the more specialised genera longitudinal septation is more regular. In *Cladostephus verticillatus* ((52) p. 508) the formation of quadrants and the subsequent periclinal division (fig. 94 H) is followed by abundant and rather irregular longitudinal septation of the inner cells, though crosswise division is frequent (fig. 94 I). In the larger branches of *Halopteris scoparia* ((46) p. 360) the perpendicular septa of the quadrant division (fig. 93 A, *1*, *2*), the first (*1*) of which lies approximately in the plane of branching, are followed by further septa (*3*, *4*) parallel to the previous ones; each quadrant thus undergoes regular crosswise division

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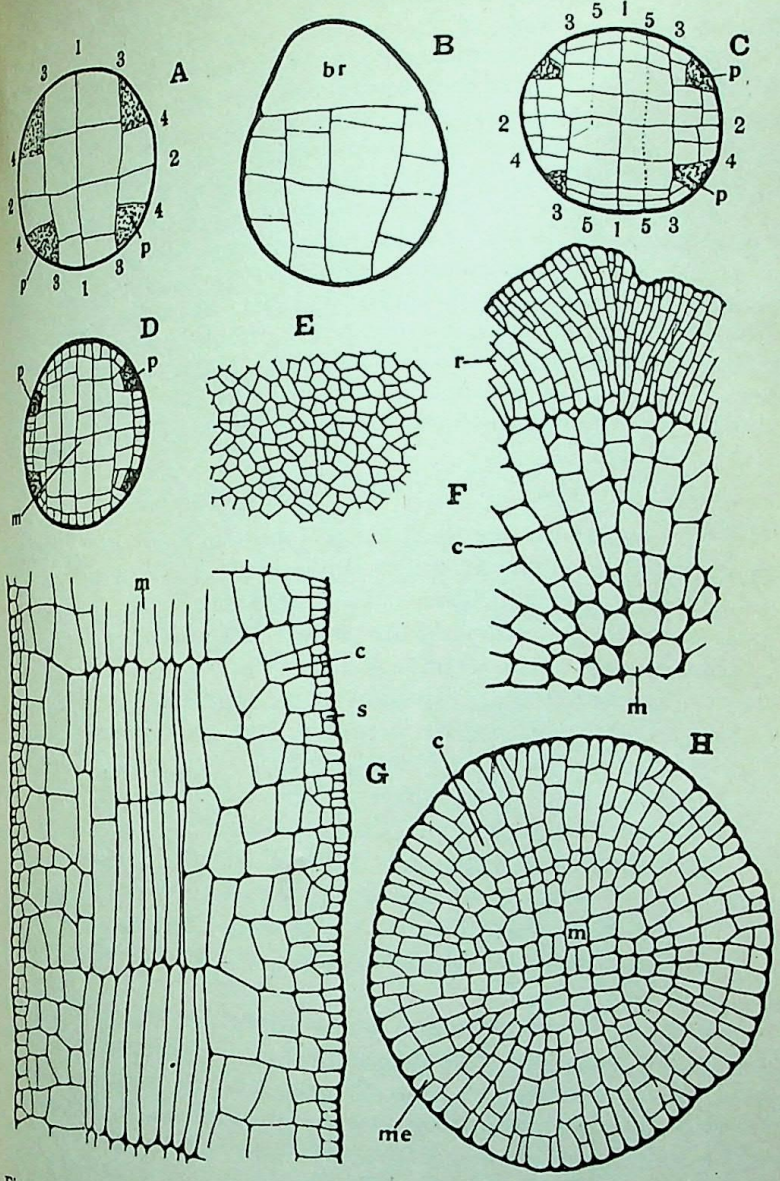

Fig. 93. A–D, *Halopteris scoparia* (Kütz.) Sauv., transverse sections of a larger axis at successively lower levels, the numerals in A and C indicating the successive walls. E–H, *Phloeocaulon foecundum* Sauv., shoot of unlimited growth; E, surface-view at the same level as G; F, transverse section of basal part showing the rhizoidal cortex (*r*); G, longitudinal section, a little way above the base; H, transverse section, a few millimetres below the summit. *br*, branch; *c*, cortex; *m*, medulla; *me*, meristoderm; *p*, pericyst; *s*, surface-layer. (After Sauvageau.)

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so that there result four central and twelve peripheral cells. Four of the latter (*p*), which appear triangular in the transverse section, constitute delayed branch-initials or rhizogenous cells (pericysts, cf. p. 270). Further septa (5), perpendicular to the third and fourth (fig. 93 C), result in a crosswise division of each central cell, as well as of each of the eight non-triangular peripheral cells. The 32 inner cells thus produced usually undergo no further longitudinal division, although the peripheral ones divide by a further radial wall (fig. 93 D).

The branches of limited growth of *H. scoparia* show a modified segmentation and no pericysts are formed. After the quadrant division there is periclinal segmentation leading to the delimitation of a peripheral layer. In the finer branches periclinal division may set in from the first so that the centre is occupied by a single large cell. This recalls the segmentation of *Sphacelaria*, and is probably found in the smaller branches of most of the more specialised members in which the major axes possess a complex structure similar to that of *Halopteris scoparia*.[1]

(*b*) Cortex-formation

The only means of secondary enlargement in leptocaulous forms is by cortication. In auxocaulous Sphacelariales, however, the peripheral layer sooner or later becomes meristematic (fig. 93 H, *me*) and gives rise to a *secondary cortex*, which is responsible for the later increase in girth. This secondary activity as a general rule appears to set in only after primary division of the segments has ceased. It is little marked in *Halopteris hordacea*, but much more evident in *Phloeocaulon* ((46) p. 445), *Ptilopogon* (fig. 103 I, *c*; (46) p. 473), and *Cladostephus* ((52) p. 509), where it follows upon the marked growth in length above referred to. The peripheral layer then becomes a meristoderm (p. 226), the cells of which divide by successive periclinal walls to form a radially arranged secondary cortex (fig. 93 G, H, *c*; 94 I). Meristematic activity continues for a variable period and is finally terminated by abundant anticlinal division of the surface-cells (fig. 93 G, *s*).

In many *Sphacelarias* (e.g. *S. olivacea*) the tiers remain recognisable throughout the plant, but in others they are obscured in the older parts by the production from the surface-cells of closely apposed, downwardly growing cortical threads (fig. 94 A, B, *r*). The extent of their development evidently varies not only with the species, but also in different individuals. Certain species (*S. plumula*, (41) p. 102) produce only few of these threads which form but an imperfect investment, but in *S. plumigera* ((41) p. 114, cf. also (35) pl. 47), for example, they are so numerous and copiously branched that they ultimately form a dense several-layered investment (fig. 94 F, *r*) which envelopes the parent axis (*a*) and the lower parts of the laterals (*l*) and may be as thick as the parts covered. In this species the cortical

[1] For further details, see (31) p. 144, (46) pp. 390, 401, 415, 423, 445.

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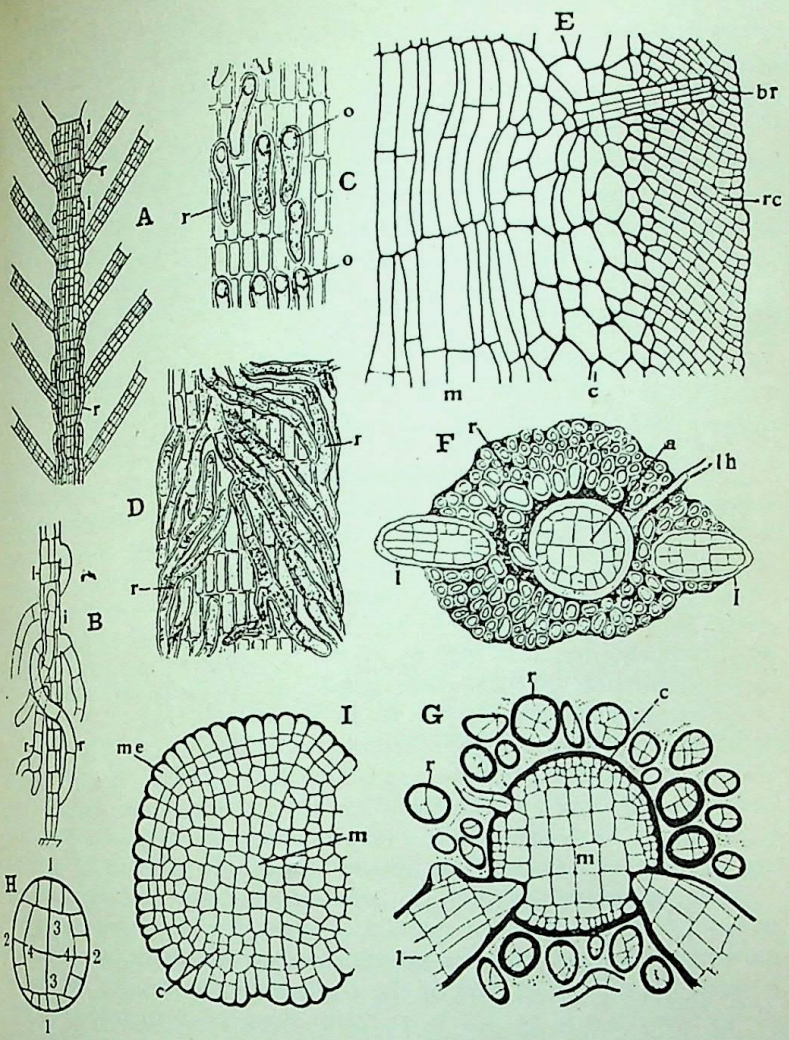

Fig. 94. A, F, *Sphacelaria plumigera* Holmes; A, cortex-formation in shoot of unlimited growth; F, section of older part of same, with two buried laterals. B, *S. hystrix* Suhr, basal part of erect axis, with rhizoids. C, D, *Chaetopteris plumosa* Kütz., two stages in cortex-formation. E, H, I, *Cladostephus verticillatus* Ag.; E, part of longitudinal section of shoot of unlimited growth, a little way above the basal disc; H, I, transverse sections of such a shoot at a considerably higher level, H near the apex, the numerals indicating the successive walls. G, *Halopteris scoparia* (Kütz.) Sauv., transverse section near base of a shoot of unlimited growth, showing rhizoids and two laterals. *a*, axis; *br*, branch; *c*, cortex; *i*, inferior secondary segment; *l*, lateral; *lh*, lateral hair; *m*, medulla; *me*, meristoderm; *o*, areas through which rhizoids arise; *r*, rhizoids or cortical threads; *rc*, rhizoidal cortex. (C, D, F after Reinke; the rest after Sauvageau.)

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threads originate from definite peripheral cells (fig. 94 A) which lie in the plane of branching and are situated in the upper half of the inferior secondary segments (*i*). Many of these cortical threads extend to the basal system and, spreading over it, contribute to its efficiency as an attaching organ.

The thick cortex of *Chaetopteris* ((27) p. 133), which encases the bases of the laterals (fig. 101 K), is composed of closely approximated threads growing obliquely downwards and again in part functioning in attachment. They arise without regularity from peripheral cells (fig. 94 C, D) of both the superior and inferior segments, thin circular areas (*o*) in the thick outer walls of these cells becoming protruded to form the threads ((33) p. 18, (35) pl. 49). The peripheral cells of the dense pseudo-parenchyma formed by the richly branched threads subsequently give rise to the fructifying branches (p. 287). *Cladostephus* possesses a similar cortex (fig. 94 E, *rc*; see below).

The four triangular peripheral cells (fig. 93 A, *p*) formed during segmentation in *Halopteris scoparia* (p. 268) usually constitute, with or without further division, initials either of late-formed branches or of rhizoids. These cells, called *pericysts* by Sauvageau ((46) pp. 350, 360; cf. also (12) p. 496), possess denser cytoplasmic contents and larger nuclei than the adjacent cells and usually occupy the complete height of a secondary segment (fig. 95 H, *p*). In the lower part of the plant a large proportion of these cells grow out into rhizoids, although the latter sometimes originate (fig. 95 H, *r*) from the base of a branch. The well-branched rhizoids of *H. scoparia* acquire thick walls and undergo transverse and longitudinal septation (fig. 94 G, *r*). They gradually cover the older parts with a loose spongy envelope which extends to the substratum. Similar features are met with in other species of *Halopteris*, e.g. *H. hordacea* ((46) p. 422) and *H. funicularis* ((33) p. 23).

The secondary increase in thickness of the auxocaulous forms described above does not usually take place in the basal parts of the main axes where mechanical strength is attained by the formation of an investment similar to that of the leptocaulous types. In *Phloeocaulon foecundum*[1] ((33) p. 31, (46) p. 447), for instance, a number of the peripheral cells grow out into branching filaments which appear to be fused from the first (fig. 93 F, *r*); the radial files in this extensive pseudo-parenchyma are slightly deflected in the longitudinal direction. Except for the apparent fusion of the threads there is much resemblance to the cortex of *Chaetopteris*. A similar, but more extensive, envelope (figs. 94 E, *rc*; 98 F, *c*) is formed in *Cladostephus verticillatus* ((33) p. 19), but here it arises also from the peripheral layer of the secondary cortex ((52) p. 520). Both here and in *Ptilopogon*, Sauvageau ((46) p. 474) finds evidence of an intermittent formation of the cortex; this is most pronounced in the latter genus, where the consecutive strata are delimited by marked thickening of the membrane of the outermost cells.

[1] According to Reinke ((33) p. 29) this investment is not formed in *P. squamulosum* Suhr (cf. however (46) p. 465).

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(c) The Method of Branching

In *Sphacelaria* (fig. 92 C, *br*) and *Chaetopteris* (fig. 101 K; (12) p. 512) the laterals, whether of definite or indefinite growth, almost invariably arise from a cell occupying the whole height of a superior segment, or in other words half the length of a primary segment. Such branching is described as *hemiblastic* by Sauvageau ((43) p. 332). The insertion of the branch on the parent axis is limited above by a primary and below by a secondary septum. The branch-initials are probably for the most part peripheral cells, which cease to segment at an early stage, but they may consist of entire sectors. Pringsheim ((31) p. 178) concluded that the initials were nearly always entire quadrants, but according to Sauvageau this is rarely so. In species with pinnate branching (*S. plumigera*, fig. 94 A; *S. plumula*, fig. 92 C; *Chaetopteris plumosa*) practically every superior segment produces a pair of functional branch-initials which usually grow out at an early stage, but when branching is less plentiful, a large number of the initials may remain dormant for a longer or shorter period. These dormant initials are often readily recognisable in *Sphacelaria*, especially in species in which the secondary segments undergo abundant septation, as larger cells with denser contents (*pericysts*, (40) p. 314) which do not exhibit transverse division (fig. 92 E, *p*); they frequently contain the same brown contents as the apical cells. In *S. radicans* and *S. olivacea* such dormant initials are present in each superior segment ((41) pp. 30, 57); in the former they probably grow out only in the reproductive phase ((51) p. 64).

The apical cell of the branch, formed by protrusion of the initial, segments in the customary manner (fig. 92 C). In the laterals of limited growth the apical cells ultimately cease to function, either persisting as pointed cells (*S. plumula*, fig. 92 D) or dividing by variously orientated walls (*S. radicans*). In *Sphacella* the branches arise as outgrowths from the upper ends of the cells (fig. 92 B).

In certain species of *Sphacelaria* (e.g. *S. hystrix*, *S. plumula*, *S. tribuloides*, fig. 95 A–C), as well as in *Chaetopteris* ((43) p. 85), the branches of limited growth bear colourless sheathed hairs (*h*) which are usually inserted opposite the transverse septa. Their peculiar mode of development ((12) p. 517, (31) p. 168, (41) p. 235) shows much similarity with the method of branch-formation found in the more specialised Sphacelariales. The hair-initials are cut off as small lenticular cells (fig. 95 A, *in*), a little to one side of the tip of the apical cell (*a*). As the latter elongates, the initial comes to occupy a lateral position (fig. 95 B) so that, when the apical cell divides (fig. 95 C), the septum (*t*) meets the convex wall of the initial approximately at right angles. Hence the position of the mature hairs opposite the septa. Sometimes the initial divides in the plane of branching (*S. radicans*, (41) p. 32) and forms two hairs, or division may go further resulting in a tuft.

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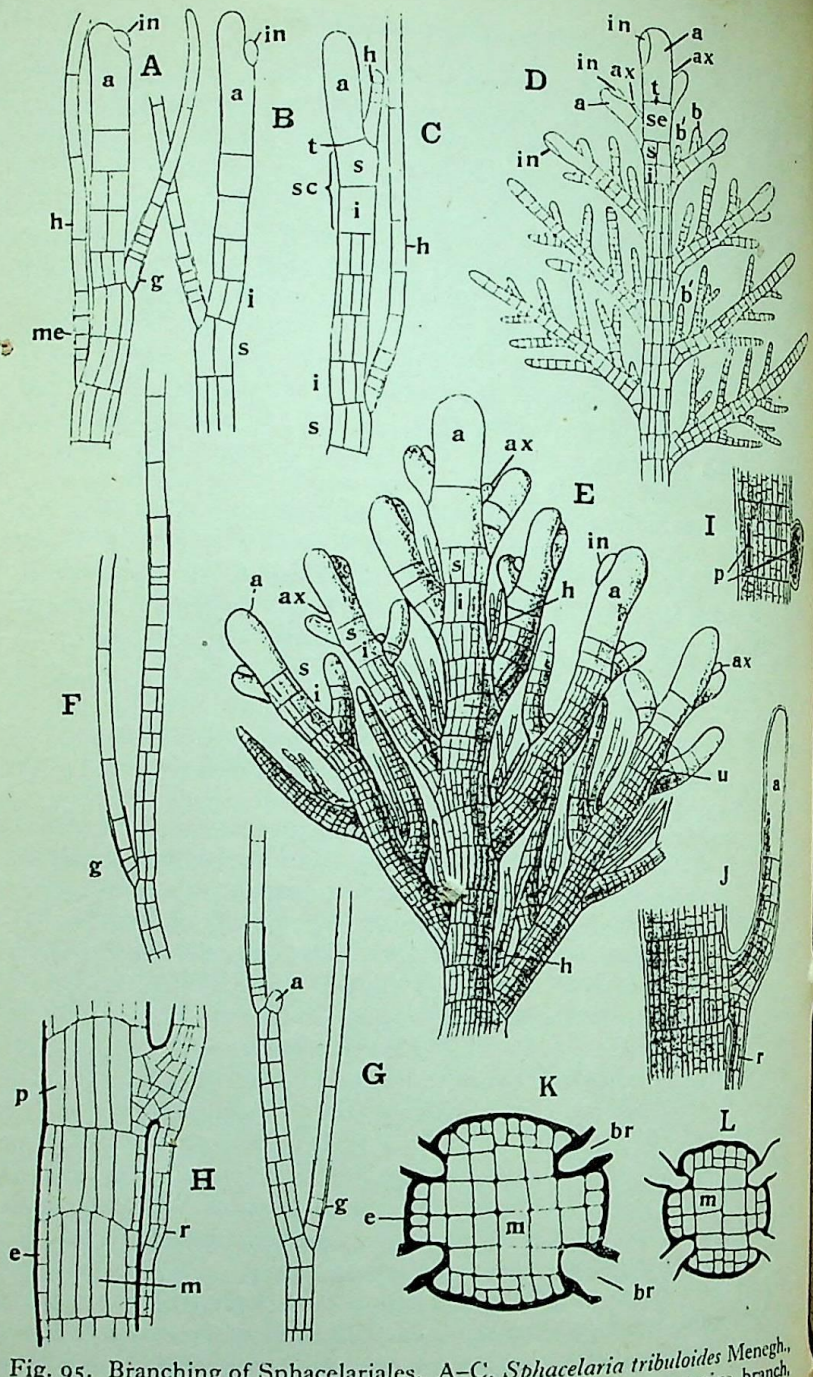

Fig. 95. Branching of Sphacelariales. A–C, *Sphacelaria tribuloides* Menegh., hair-formation. D, *Halopteris filicina* Kütz., apex of a vegetative branch, showing method of branching. E, *H. scoparia* (Kütz.) Sauv., ditto. F, G, *Sphacelaria furcigera* Kütz., terminal and lateral hairs. H–L, *Halopteris*

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If the apical cell ceases growth after the formation of the initial, the hair remains in an apical position (fig. 95 G) and may be actually terminal (*S. plumula*, *S. furcigera*, fig. 95 F; (41) pp. 98, 372). In *Alethocladus* (43) pp. 337, 346), which lacks the hairs found in most of the more specialised Sphacelariales, the lateral branches develop in identically the same way as these hairs of *Sphacelaria*. The laterals consequently lie opposite the primary septa, their bases later extending onto the inferior segment above and the superior segment below (cf. fig. 97 D).

The process of hair-formation in *Sphacelaria*, as well as the method of branching found in the more specialised Sphacelariales (cf. below), is interpreted by Magnus ((27) p. 146) and Sauvageau as sympodial in nature. The lenticular hair- or branch-initial (fig. 95 A, B, D, *in*) is regarded as the actual apical cell, while the large remaining portion (*a*) of the original apical cell, which segments to form the continuation of the axis, is looked upon as a branch. Since this develops from the entire segment of the apical cell, this method of branching is styled *holoblastic* by Sauvageau; it differs from the hemiblastic type also in the oblique position of the septum. The main axes of *Alethocladus* are, on this interpretation, sympodia, comprising as many sections as there are laterals, each of the latter representing the actual termination of the underlying segment of the sympodium. Similarly, the above-described hairs of *Sphacelaria* are regarded as terminal and the axis bearing them as a sympodium, the successive joints of which are terminated by the hairs. The transverse septum, which abuts on the hair-initial of a *Sphacelaria* or the branch-initial of *Alethocladus*, divides the original apical cell into a lower primary segment (fig. 95 C, *sc*), belonging to the joint terminated by the hair or branch, and an upper segment (*a*) constituting the apical cell of a new joint of the sympodium.

As evidence in support of this interpretation Sauvageau ((41) p. 238) cites those instances in which such initials develop into terminal hairs (fig. 95 F). The hair then occupies its normal position at the apex of the axis. Further support for the hypothesis is to be found in the details of propagule-formation in *Sphacelaria* (p. 285). The correctness of this interpretation is disputed by Reinke and Pringsheim ((33), (31) p. 150).

The holoblastic branching of *Halopteris*, *Phloeocaulon* and

funicularis (Mont.) Sauv.; H, J, hemiblastic branching and rhizoid-formation; I, outgrowing pericyst; K, L, transverse sections of long axes, showing formation of hemiblastic branches. *a*, apical cell; *ax*, axillary initial; *b*, *br*, branches; *e*, surface-layer of thallus; *g*, sheath of hair; *h*, hair; *i*, inferior secondary segment; *in*, initial; *m*, medulla; *me*, meristoderm; *p*, pericyst; *r*, thizoid; *s*, superior secondary segment; *sc*, primary segment; *se*, segment; *t*, septum; *u*, shoot of unlimited growth. (D after Goebel; E, I, J after Reinke; the rest after Sauvageau.)

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Ptilopogon shows greater complexity.[1] Here (fig. 95 D) the branch-initial (*in*) at an early stage divides horizontally and cuts off a small cell (*ax*) on its upper side. According to Sauvageau's interpretation ((43) p. 334) the latter (*ax*) is the true apical cell, while the lower larger cell represents its only segment which elongates and divides to form the branch; in other words this branch is actually a lateral of a diminutive axis capped by the cell *ax*. The septum (*t*), arising in the original apical cell (*a*) of the axis, again abuts on the lenticular branch-initial, but always on its lower larger segment. As this lengthens and divides to form the branch, the overlying cell (*ax*) remains in its axil (fig. 95 D, the topmost branch on the left), and in the further course of events either remains arrested or develops in diverse ways into hairs (fig. 95 E, *h*) or reproductive organs (fig. 102 C). It is the presence of such axillary growths that distinguishes *Halopteris*, etc. from *Alethocladus*. The laterals of limited and unlimited growth arise in the same way ((31) p. 150). Branching in the holoblastic types is necessarily alternate (fig. 95 D, E) and, if hairs are present, they are always axillary in position. The successive apical cells either cut off several ordinary segments between the intervals of branch-formation or only one segment is formed (*Halopteris filicina*, fig. 95 D). This determines whether the laterals are separated by marked internodes or not.

In most species of *Halopteris* (e.g. *H. scoparia*) the axillary cell divides and gives rise to a tuft of hairs (fig. 95 E, *h*). *H. filicina* is, however, distinguished by the usual absence of hairs ((12) p. 504, (33) p. 20) and by the fact that, although the numerous laterals of a given axis are for the most part arranged in two alternating rows, as in other species of the genus, the first two are usually both situated on the adaxial side, the lowest not uncommonly appearing in a pseudo-axillary position (fig. 95 D, *b'*). This is because, in *H. filicina*, the axillary cell mostly develops into a branch (*b'*) resembling the next one (*b*), which is as usual (cf. fig. 95 E) produced on the adaxial side. In occasional individuals, however, the axillary branch may be replaced by hairs.

In *Phloeocaulon* ((12) p. 509, (46) p. 442) the axillary initial gives rise to a group of cells which soon disorganise, while in *Ptilopogon* it produces a cushion of cells which remain dormant until the time of fruiting (p. 289).

Branching in these holoblastic forms may also be hemiblastic, although laterals formed by the latter method often appear only in older plants. They originate, as in a *Sphacelaria*, from dormant initials (pericysts) formed at an early stage in the segments of the apical cell (cf. p. 270). Such branching has not been observed in *Halopteris filicina*, but is frequent in *H. scoparia*, *H. funicularis* (fig. 95 H–L) and *Ptilopogon*; in the last some of the fruiting branches are probably produced in this way. Most authorities ((31) p. 151, (33) p. 23, (40) p. 436) speak of these branches as adventitious, but one must agree

[1] Some of the details given by Geyler ((12) p. 484) are erroneous.

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with Oltmanns ((29) p. 94) in questioning the validity of such a term; despite their tardy outgrowth, they are primary in origin.

Whatever attitude may be taken towards the interpretations of Magnus and Sauvageau, it is manifest that the origin of the branch-initials in *Halopteris*, *Phloeocaulon*, and *Ptilopogon*, from small segments of the apical cell itself, results in these genera in a distinct type of morphological construction. The hemiblastic mode of branch-formation is probably to be regarded as primary, while the holoblastic method was perhaps initiated in connection with hair-development.[1] A subsequent modification resulted in the cutting off from the hair-initial of a segment which could grow out into a lateral, giving the mode of branch-formation found in most species of *Halopteris* where, however, it is still accompanied by the development of hemiblastic branches (cf. above and fig. 95 H–L). *H. filicina*, which apparently no longer has the capacity for hemiblastic branch-formation, would thus represent the most specialised member of its genus, and it is significant in this connection that the axillary hairs of the other species are here usually replaced by a branch (fig. 95 D). *Alethocladus* would represent the culmination of this line of development, since here the tendency of the initial to give rise to a hair is completely lost.

In *Cladostephus verticillatus* ((12) p. 520, (27) p. 137, (31) p. 152, (47), (52) p. 506) the first whorls of laterals of limited growth arise a little way behind the apex by the protrusion of peripheral cells of the superior secondary segments (figs. 96 A; 97 G, *br*); the members of a whorl do not all necessarily develop at the same time. The first segment or segments, cut off from the apical cells thus constituted, become part of the axis and undergo copious division (fig. 96 A) to form a cushion of tissue (*b*). In transverse sections through older whorls (fig. 97 G) the interspaces between the individual members (*br*) are occupied by a tissue (*c*) which by degrees completely envelopes their bases and is formed ((52) pp. 512, 518) by radial elongation and periclinal division of the peripheral cells situated just above a young whorl, the rows of cells thus produced being slightly deflected in the downward direction.

As a result of the abundant septation and elongation taking place behind the apex (p. 265), the older whorls appear to arise only from the summits of the superior segments (fig. 96 B), although originally hemiblastic in origin. The peripheral tissue occupying the lower portions of these segments (fig. 96 B, *b*)—actually representing the bases of the primary branches—sooner or later gives rise to other

[1] Sauvageau ((51) p. 67) records the absence of all hemiblastic branching in individuals of *Sphacelaria radicans* grown in cultures. These produced abundant hairs and some showed holoblastic branching in relation to the latter. These data indicate that the capacity for holoblastic branching exists also in *Sphacelaria* and that it is combined with a suppression of the usual hemiblastic method.

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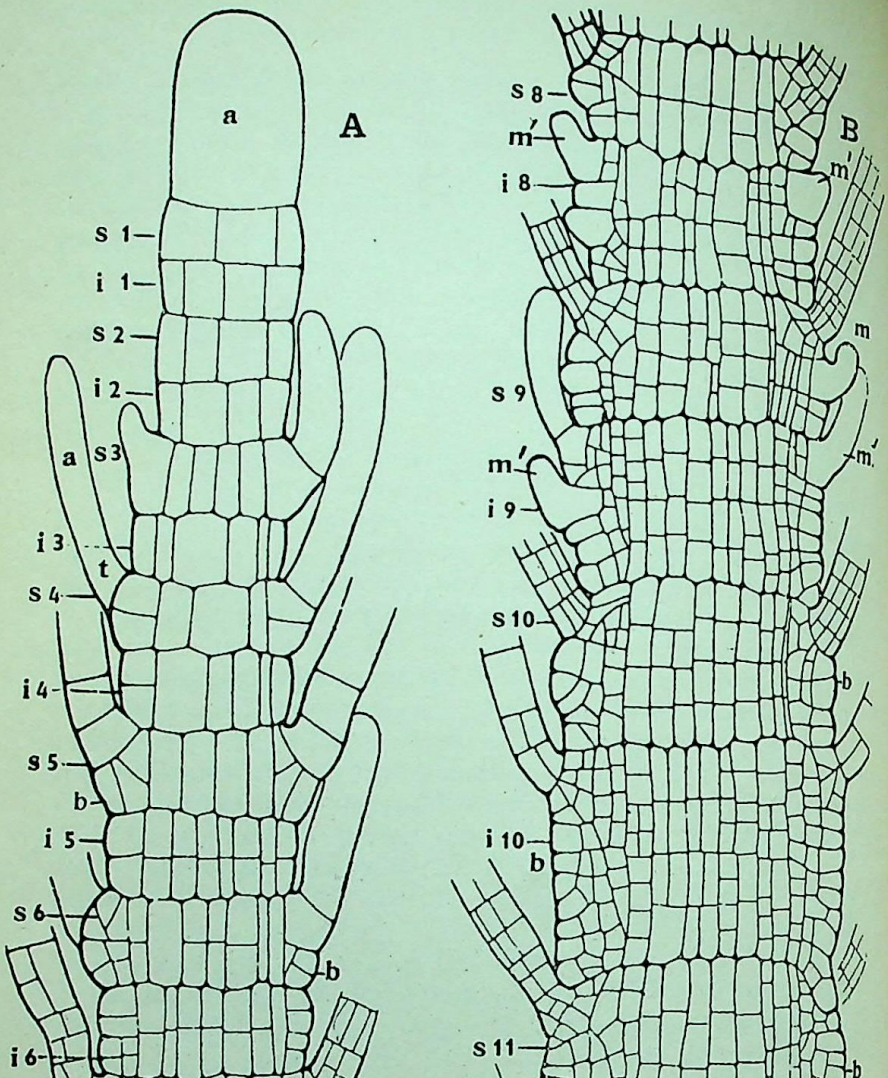

Fig. 96. *Cladostephus verticillatus* Ag., longitudinal section of a shoot of unlimited growth (after Sauvageau); the successive superior (*s*) and inferior (*i*) secondary segments are numbered. *a*, apical cell; *b*, cushion of tissue formed at base of lateral; *m*, *m′*, secondary laterals (see text); *t*, septum demarcating apical cell of lateral.

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whorls of laterals (fig. 96 B, *m*). Since these originate only from a part of the secondary segment, they are spoken of as *meriblastic* by Sauvageau ((52) p. 515). Other secondary whorls, in part often incomplete, subsequently arise from the peripheral cells of the secondary inferior segments (*m'*). Despite its whorled branching and other specialised features, *Cladostephus* approaches closely to *Sphacelaria* in the mode of formation of the primary laterals and probably represents a separate evolutionary line.

The long branches of *Cladostephus*, which commonly form a dichotomising system (fig. 91 F), are hemiblastic in origin. The initials, constituted by one of the first-formed peripheral cells of a superior segment, do not undergo the anticlinal divisions seen in the adjacent cells (fig. 97 H, *ls*); they thus correspond to a number of the initials forming the laterals of limited growth (*plagioblastic* (52) p. 528). Pringsheim ((31) p. 148) concluded that branching of the long axes was dichotomous, but, according to Sauvageau ((52) p. 526), the segmentation he describes occurs only if the apical cell is damaged (p. 279).

The laterals of limited growth do not exhibit the secondary increase in girth shown by the long axes. The members of the first and last whorls formed in any given season are simple, while the intermediate ones are more or less strongly branched ((52) p. 532), the branches being commonly situated on the abaxial side. This branching is always holoblastic (fig. 97 A–C), with formation of axillary hairs, as in *Halopteris* (fig. 97 D, E, *h*); similar shoots of limited growth may arise direct from the basal disc. The axillary hairs usually occur in two pairs (fig. 97 D, E), the one in front of the other, the two members of a pair lying in a plane perpendicular to that of the branching of the lateral. Each pair of hairs originates from a separate lenticular cell (fig. 97 C, *ax 1*, *ax 2*), the two cells being cut off successively from the branch-initial ((52) p. 537). Sauvageau describes numerous modifications of the normal plan.

Dichotomous branching is characteristic of the monotypic *Disphacella* ((43) pp. 338, 342) which is imperfectly known. Branching is initiated by the apical cell becoming bilobed; a longitudinal wall then separates the lobes which constitute two apical cells. The structure of the axes resembles that of the simpler *Sphacelarias* and pericysts are differentiated which rather exceptionally grow out into branches. Oltmanns ((29) p. 90) suggests that this may be an abnormal form.

The diverse methods of branching typical of the mature plant of Sphacelariales undergo some modification as a result of damage to one of the major axes or when the latter die back in the autumn ((41) p. 99, (43) p. 82). In *S. radicans* Sauvageau ((51) p. 64) records an apparently natural truncation of all the erect shoots which is followed by the outgrowth of dormant branch-initials into laterals bearing the reproductive organs. When the upper part of an erect shoot is removed, one or more of the youngest laterals carry on the growth or a new shoot arises from the adjacent inferior segment. If the remaining part bears mature laterals only, the intact cells at the exposed surface can grow out into

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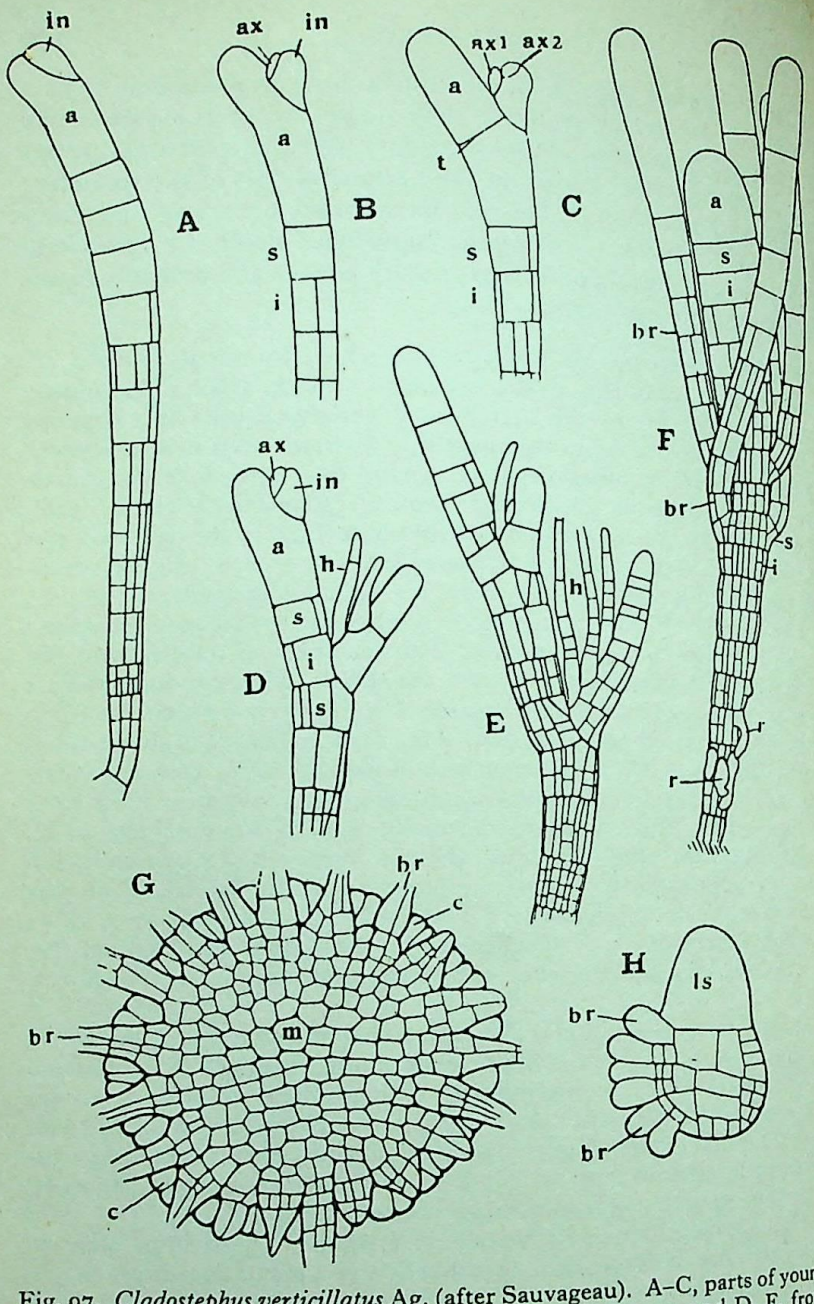

Fig. 97. *Cladostephus verticillatus* Ag. (after Sauvageau). A–C, parts of young shoots of limited growth, produced on the prostrate system, and D, E, from a young whorl, showing branch-formation; F, young shoot of unlimited growth developed from the prostrate system; G, transverse section through a shoot of unlimited growth, passing through a whorl of laterals; H, ditto through a younger region, showing origin of a shoot of unlimited growth (*ls*). *a*, apical cell; *ax*, *ax* 1, *ax* 2, axillary initials; *br*, branch; *c*, cortex; *h*, hair; *i*, inferior and *s*, superior secondary segment; *in*, initial; *m*, medulla; *r*, rhizoid; *t*, septum.

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new shoots. Such regeneration from the stumps of shed laterals is partly responsible for the fastigiate habit sometimes shown by *Halopteris scoparia* (fig. 91 D; (15) p. 347, (46) p. 355). Production of adventitious growths from the remains of the fruiting axes of the previous season is also seen in *Cladostephus verticillatus* ((31) p. 162, (52) p. 530), where the medullary cells at the exposed surface grow out into branches (cf. fig. 106 A, *p*).

Damaged apical cells of *Sphacelaria* are regenerated from the underlying segment ((66) p. 152). If this has undergone transverse division only, the upper half constitutes a new apical cell, while if longitudinal walls have already arisen one of the resulting cells grows out laterally into a new apex. Inferior segments, if they have already divided longitudinally, cannot produce a new apex, which is then formed from the underlying superior segment. According to Sauvageau ((52) p. 530) damage to the apical cell of *Cladostephus* often leads to the regeneration of two new apicals, resulting in the dichotomous branching described by Pringsheim ((31) p. 148) as a normal phenomenon. If the apical cell of *Sphacelaria* is exposed to a low light-intensity, it grows out into a rhizoid (inversion of polarity, (66) p. 165).

THE PROSTRATE SYSTEM

A well-developed discoid prostrate system is probably typical for the order. Good examples are seen in many species of *Sphacelaria* (e.g. *S. olivacea*, figs. 98 B, C; 99 B; (35) pl. 46; *S. plumigera* (41) p. 114), as well as in *Phloeocaulon* and *Chaetopteris* ((33) p. 17). In all of these the erect shoots arise from a basal crust which consists of several layers and exhibits marginal growth (fig. 98 B, *m*). Viewed from below (fig. 98 B) the basal layer appears as a system of radiating coalescent filaments, which give rise to approximately vertical files of cells forming the crust (fig. 98 I); there is considerable resemblance to a *Ralfsia* or *Lithoderma*. As already noted (p. 270) these crusts are strengthened by the downgrowth of rhizoids from the erect axes. Not uncommonly several crusts grow over one another (fig. 98 G). The superjacent strata often belong to distinct individuals, but they may also be due to the outgrowth of surface-cells from older crusts which, spreading over the latter, produce a new superposed stratum. Very elaborate crusts of this kind are formed in *Cladostephus verticillatus* (p. 282). Foreign Algae are sometimes enclosed between the successive strata ((41) p. 58).

The thick crusts just described are probably always perennial, and the species of *Sphacelaria* possessing them rarely form propagules ((43) p. 79);[1] all of them show transverse septation of the secondary segments. The bases of the erect axes are invariably buried amid the

[1] Perennation is, however, impossible in epiphytic or endophytic forms in which, during part of the year, the host is lacking or sheds the parts upon which the former occur. The mode of persistence of such species is not yet clear (cf. (6), (45)).

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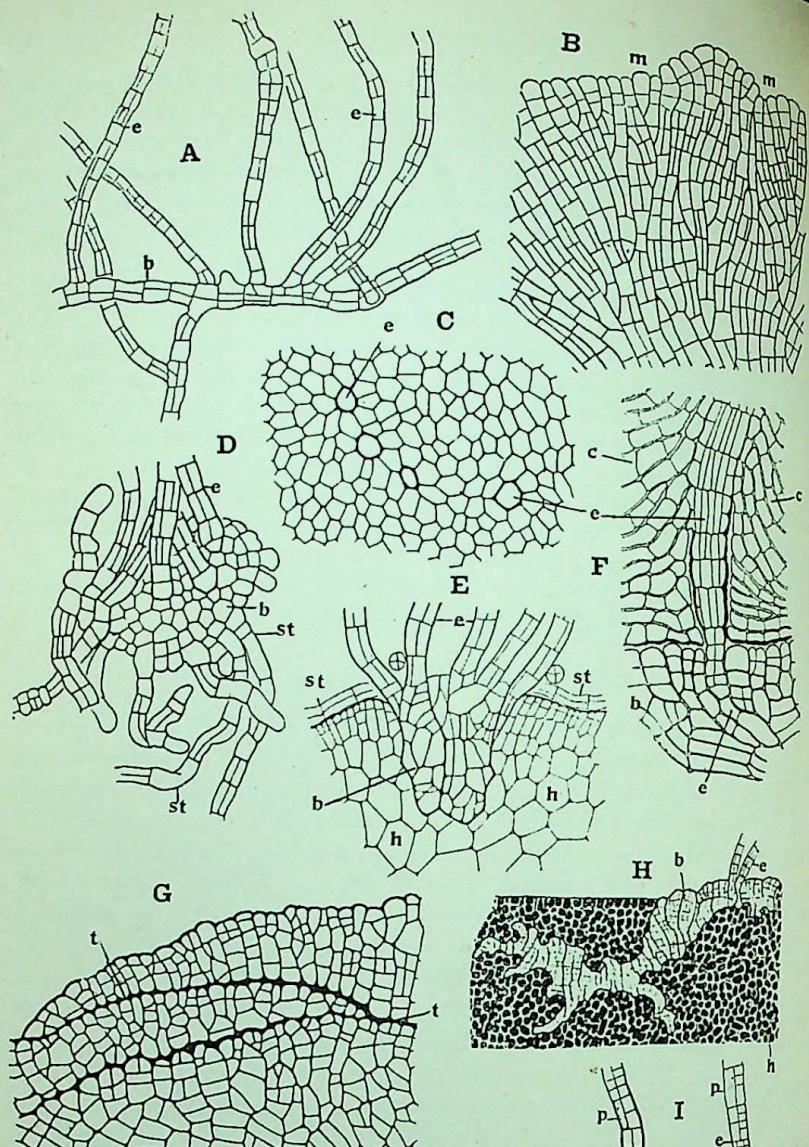

Fig. 98. Prostrate system of Sphacelariales. A, *Sphacelaria britannica* Sauv., B, C, I, *S. olivacea* Pringsh.; B, the crust from below; C, the same from above; I, vertical section showing origin of two erect threads. D, *S. radicans* Harv., basal system with stolons (*st*). E, *S. bipinnata* Sauv., endophytic basal system (*b*) and epiphytic stolons (*st*) on *Halidrys*. F, G, *Cladostephus verticillatus* Ag.; F, vertical section of crust (*b*) showing origin of an erect axis (*e*); G, vertical section of compound crust. H, *S. caespitula* Lyngb., showing the endophytic basal system (*b*). *b*, prostrate and *e*, erect systems; *c*, cortex; *h*, host; *m*, marginal meristem; *p*, pericyst; *st*, stolon; *t*, limits of crusts. (F, H after Reinke; the rest after Sauvageau.)

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vertical rows of the crust (fig. 98 F, I, *e*) so that the upright shoots represent a further development of certain of the latter.

Basal discs of the type just described are rarely met with in *Halopteris* ((46) p. 337), in most species of which the corticating threads envelop the bases of the axes with a spongy mass of considerable width, a condition well seen in *H. scoparia* ((46) p. 356). The individual threads spread over the substratum. A less highly differentiated prostrate system is also found in diverse epiphytic *Sphacelarias*. In *S. cirrhosa*, for instance, the disc consists of a single layer of cells ((42) p. 404), whilst in *S. plumula* the short irregular filaments of which it is composed are only partly coalescent ((41) p. 102). In the endophytic species the prostrate system generally consists of loosely branched threads (*S. pulvinata*), which sometimes form bundles (*S. Reinkei*) penetrating to some depth into the substratum (cf. fig. 98 E, *b*). Other endophytes possess an epiphytic disc, bearing branches which penetrate into the host (e.g. *S. Novae Caledoniae* (41) p. 252). *S. caespitula* Lyngb. ((33) p. 13) forms a several-layered crust of uneven thickness (fig. 98 H, *b*) within the tissues of *Laminaria Cloustoni* and *Saccorhiza bulbosa*; the little-branched erect threads serve mainly to bear the reproductive organs. In *Sphacella*, inhabiting *Carpomitra costata*, the endophytic system varies (cf. (33) p. 6, (40) p. 229).

Reduction of the erect system is commonly encountered among the endophytic *Sphacelarias*, but may occur also in epiphytic species like *S. olivacea* (fig. 99 B). Here the plant is at times represented solely by the basal crust ((41) p. 56)—a stage described by Kuckuck ((21) p. 232) as a distinct genus *Sphaceloderma*. In such instances the unilocular sporangia are borne directly on the basal stratum (fig. 99 C, D, *u*) and are the only parts of the erect system present.

The rare lithophyte *Battersia* ((33) p. 4, (40) p. 224), first discovered at Berwick-on-Tweed, may be a similar reduced state of some *Sphacelaria*, although at present there is no evidence to prove that it is not an independent genus ((43) p. 80); it is certainly a reduced form. The thick, many-layered crusts (up to 4 cm. in diameter) consist of a number of separate strata (fig. 99 A, *b*), while the little-branched erect threads (*e*) exhibit apical growth and occasional longitudinal division of their cells. They bear unilocular sporangia (*u*) and are aggregated to form scattered groups.

In diverse *Sphacelarias* the basal disc plays a rôle in the spread of the individual over the substratum. Thus, in *S. radicans* ((41) p. 33) certain peripheral cells grow out into simple or branched horizontal stolons (fig. 98 D, *st*) possessing the same structure as the upright threads. The tips develop into new discs which either produce erect threads or give rise to further stolons. Much the same occurs in *S. Novae Caledoniae* ((41) p. 252). In *S. cirrhosa* ((42) p. 404) some of the lower laterals may become prostrate (fig. 99 E) and form new discs (*d*) at their tips. The stolons of *S. bipinnata* (4) and *S. hystrix*

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((42) p. 334) have a different origin. Here the bases of the erect shoots, which arise from the bundle of endophytic threads (fig. 98 E, *b*), become covered with a weft of rhizoids, some of which (*st*) spread horizontally and give rise at their tips to other plants.

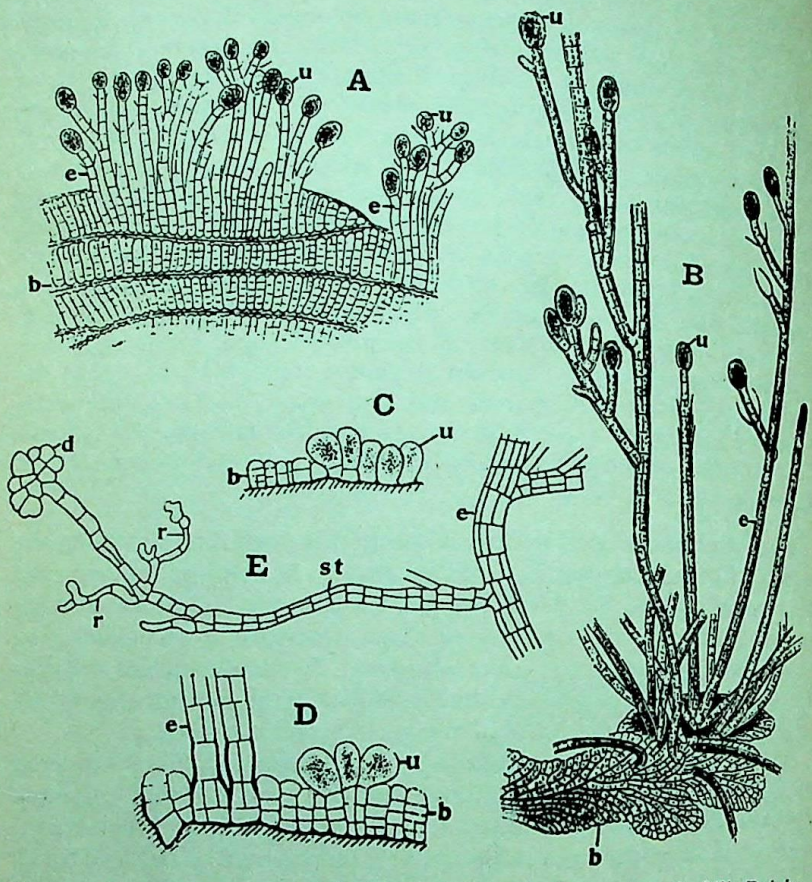

Fig. 99. Prostrate system of Sphacelariales. A, *Battersia mirabilis* Reinke, vertical section of basal crust with erect threads bearing unilocular sporangia. B–D, *Sphacelaria olivacea* Pringsh.; B, basal system with erect threads bearing unilocular sporangia; C, D, vertical sections of parts of the basal crust bearing sporangia, in D with two erect shoots. E, *S. cirrhosa* C. A. Ag., f. *meridionalis* Sauv., primary lateral functioning as a stolon. *b*, basal and *e*, erect systems; *d*, secondary disc; *r*, rhizoid; *st*, stolon; *u*, unilocular sporangium. (A, B after Reinke; C–E after Sauvageau.)

The elaborate crusts of *Cladostephus verticillatus* ((33) p. 19, (52) p. 492), which are composed of several irregularly superposed strata (fig. 98 G) delimited from one another (*t*) by strong thickening of the outer walls of the surface-cells, show a marked capacity for the formation of stolons (fig. 106 E, *st*) from the marginal and superficial cells. These produce new crusts at their tips or along their length,

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while some of them grow on to the parent crust and contribute a further stratum. According to Sauvageau the erect axes of this species always arise from stolons.

VEGETATIVE REPRODUCTION

The stolons described above serve as a means of local vegetative reproduction, but many species of *Sphacelaria* possess propagules of characteristic form (fig. 91 B, *p*), which constitute an efficient method of dispersal. In several, propagules are produced far more frequently than sporangia, and such species evidently rely largely on this method of reproduction ((43) p. 87). Propagules and sporangia may be formed in different seasons (*S. hystrix*), while in other species they occur simultaneously, but on different individuals (e.g. *S. furcigera*; cf. also (5) p. 46) or on different branches (e.g. *S. biradiata*). Not uncommonly, however, the two types of structures are intermingled (*S. cirrhosa*, *S. bipinnata*).

The propagules invariably arise from dormant branch-initials which are nearly always situated in the superior segments. In *S. plumula* and other species ((17), (31) p. 176, (41) p. 105) the initial of the propagule becomes protruded as an apical cell (fig. 100 A, *a*) which first cuts off a number of transverse segments (fig. 100 C–F), during which it commonly broadens. The first septum, which arises beyond the surface of the parent axis (fig. 100 B), marks the point of subsequent detachment of the propagule so that, after the latter is shed, a short stalk (sterigma of Janczewski (16, 17)) remains (fig. 92 D, *st*) from which a further propagule can develop. The subsequent segments (2 or 3 in number, fig. 100 E, F) divide into two secondary ones (*s*, *i*) in the usual way. After this the apical cell cuts off at its summit a small lenticular cell (fig. 100 F) which either undergoes no further development (*S. plumula*, *S. fusca*) or sooner or later grows out into a colourless hair (*S. biradiata*, sometimes in *S. hystrix*, fig. 100 K, M, *h*). The large remaining portion of the apical cell (fig. 100 F, *b*), which corresponds to a last primary segment, soon spreads out laterally to form the arms of the propagule (fig. 100 G) and usually divides by a median longitudinal wall.[1] Either before or after this, a curved septum arises in each arm and cuts out an apical cell (fig. 100 G, *l*) which produces two or more segments (fig. 100 H). The further subdivision of these segments and of the cells composing the body of the propagule varies according to its final shape.

According to Janczewski ((16) p. 341) detachment of the propagule is due to pressure exerted by its basal cell upon the sterigma; this

[1] Reinke's figures ((33) tab. IV, figs. 11, 12) of *S. furcigera*, which show the curved septa delimiting the apicals of the arms meeting in the centre, indicate that in this species there is no longitudinal division of the body of the slender propagule (cf. also (1) p. 21).

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causes rupture of the external membrane which forms a collar around the persisting sterigma. Each time a new propagule develops, a further sterigma is formed at its base so that, when repeated innovation has occurred, the point of insertion exhibits a series of collars.

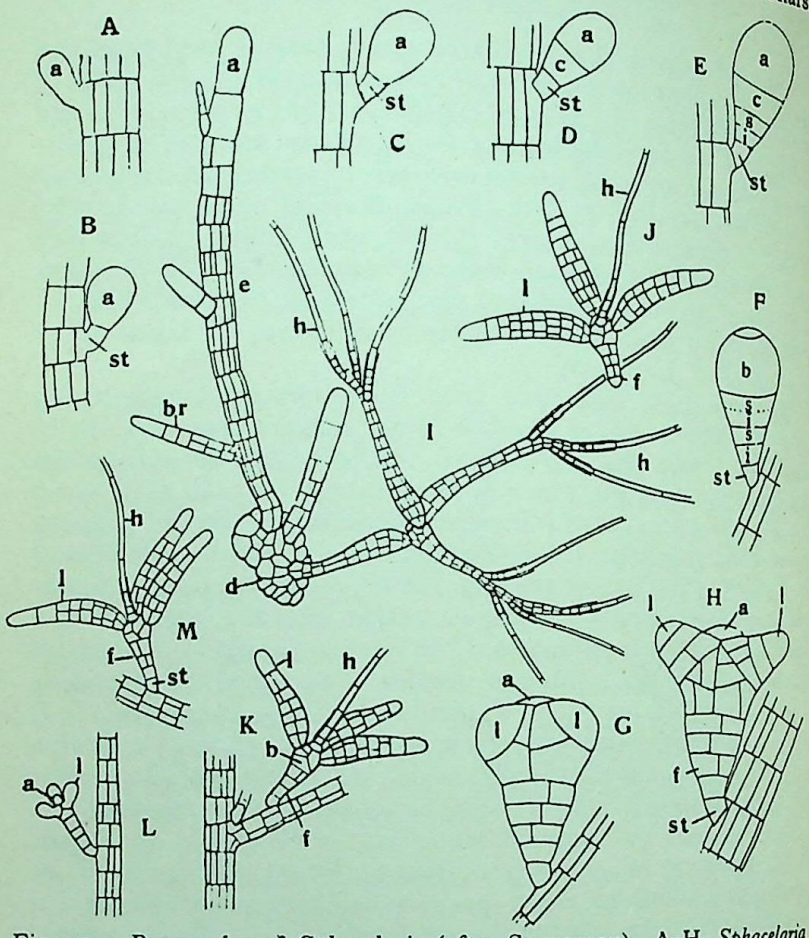

Fig. 100. Propagules of *Sphacelaria* (after Sauvageau). A–H, *Sphacelaria plumula* Zanard.; A–G, stages in the development of the propagule; H, mature propagule. I–K, *S. cirrhosa* C. A. Ag., f. *meridionalis* Sauv.; I, germinating propagule; J, K, mature propagules, in J detached, in K *in situ*. L, M, *S. hystrix* Suhr; L, young and M, mature propagules. *a*, apical cell; *b*, last and *c*, last but one segment formed in axis of propagule; *br*, branch; *d*, basal system; *e*, erect shoot; *f*, foot (pedicel) of propagule; *h*, hair; *i*, inferior and *s*, superior secondary segment; *l*, arm of propagule; *st*, sterigma.

The propagule may have the shape of a broad (*S. tribuloides*) or narrow (*S. plumula*, fig. 100 H) wedge, or the two arms may be produced and more or less cylindrical (*S. furcigera*) or fusiform (*S. biradiata*). In certain species (*S. hystrix*, fig. 100 M; *S. fusca*; *S.*

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cirrhosa, figs. 91 B, *p*; 100 J) the body of the propagule is prolonged into three arms[1] lying in different planes and the number of arms is then not uncommonly variable; there may be 2, or 4 or 5. Since the lower part (foot, fig. 100, *f*) of the propagule constitutes an additional arm, the two-armed types after detachment appear triradiate, the three-armed ones quadriradiate (fig. 100 J). In *S. furcigera* one or both of the arms may be branched, and this is more marked in *S. divaricata* Mont. ((41) p. 409), where the propagules commonly show repeated forking in one plane, each fork being surmounted by an arrested lenticular cell.[2]

The propagules are clearly modified branches. Particularly when the arms are developed as cylindrical rays, they afford a clear example of "dichasial" or "trichasial" branching which, in *S. divaricata*, may moreover take place repeatedly. As Oltmanns ((29) p. 95) points out, the mode of development of the propagules, especially in those instances in which the apical cell grows out into a hair (fig. 100 M), lends considerable support to the view that the holoblastic branching described on p. 273 is sympodial in character.

The rayed types of propagules probably float easily and will readily become anchored among surrounding algal growth, while the cuneate types being more massive perhaps harbour more reserve food ((43) p. 89). Any one of the arms (including the foot) can develop into a new plant if it comes into contact with a suitable substratum (cf. also (16) p. 343, (45) p. 312). It gives rise to a short filament which expands into a disc (fig. 100 I, *d*) from which the erect axes (*e*) arise. The arms, not in contact with the substratum, usually produce a tuft of hairs (*h*), one of which is formed from the apical initial.

No other member of the order possesses the specialised propagules met with in *Sphacelaria*, but many can probably propagate vegetatively with the help of detached branches, as has been observed in *S. plumula* ((41) p. 102), as well as in *Halopteris scoparia* ((46) p. 356). In either instance the peripheral cells of the lower segments grow out into plentiful rhizoids, and in *H. scoparia* these are stated to be capable of producing new erect axes.

THE ARRANGEMENT OF THE SPORANGIA

Both uni- and plurilocular sporangia, not uncommonly found on distinct individuals, are known in a considerable number of Sphacelariales. The two kinds of organs usually occupy a similar position, but there is much diversity in their mode of arrangement.

[1] The shape of the arms is not altogether constant. According to Sauvageau ((44) p. 199) the propagules of northern forms of *S. cirrhosa* have cylindrical arms, whilst in the more southern forms they are fusiform and tend to increase in number.

[2] In *S. olivacea* Pringsheim ((31) p. 178) recorded the development from dormant initials of grape-like clusters, assumed to play a rôle in vegetative reproduction. They have not since been observed.

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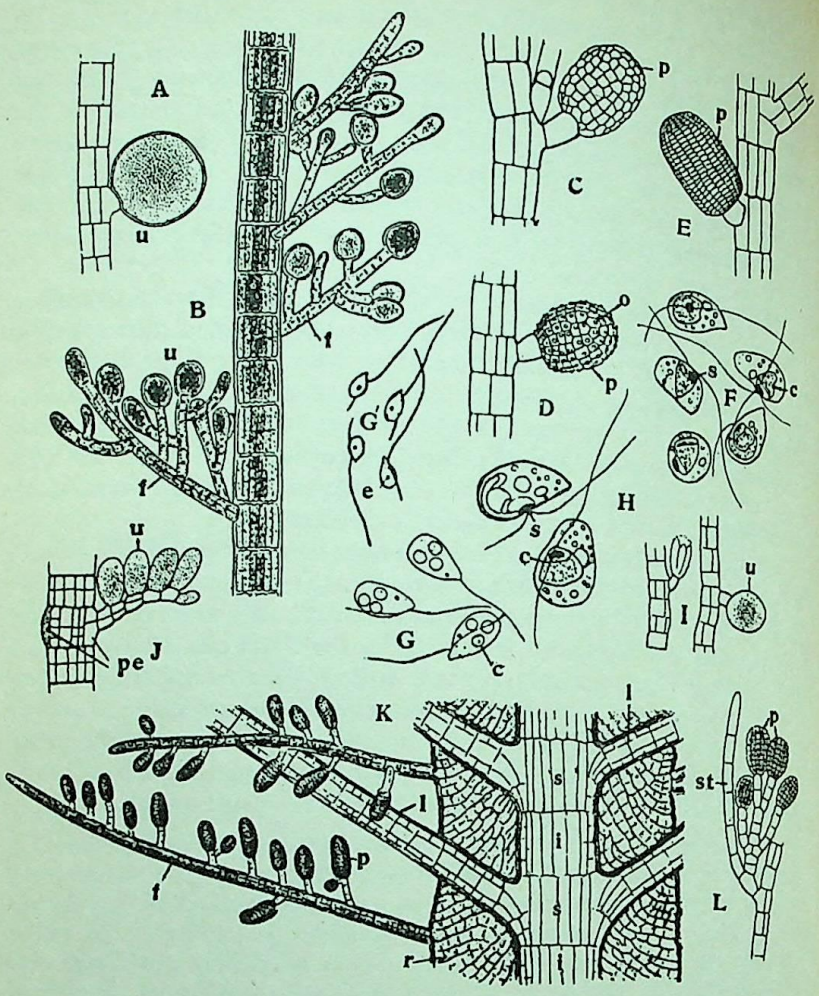

Fig. 101. Reproductive organs of *Sphacelaria* (A–E, G, L) and *Chaetopteris* (F, H, K). A, *Sphacelaria furcigera* Kütz., unilocular sporangium. B, *S. racemosa* Grev., part of erect axis with fruiting branches (*f*). C–E, G, *S. hystrix* Suhr; C, D, female (?) and E male (?) plurilocular sporangia, dehisced in D; G′, male (?) and G, female (?) swarmers from same. F, H, K, *Chaetopteris plumosa* Kütz.; F, swarmers from plurilocular and H, ditto from unilocular sporangia; K, longitudinal section of an older shoot, with fruiting branches (*f*). I, *Sphacelaria britannica* Sauv., unilocular sporangia, that on the left dehisced. J, *S. Reinkei* Sauv., branch with unilocular sporangia. L, *S. bracteata* Sauv., pseudo-axillary plurilocular sporangia. *c*, chromatophore; *e*, stigma; *f*, fruiting lateral; *i*, inferior and *s*, superior secondary segment; *l*, lateral; *o*, apertures in sporangium wall; *p*, plurilocular and *u*, unilocular sporangium; *pe*, pericyst; *r*, rhizoidal cortex; *s*, stigma; *st*, sterile lateral. (B, K after Reinke; F, H after Kuckuck; the rest after Sauvageau.)

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In *Sphacelaria* the sporangia are generally borne terminally on simple or branched laterals (fig. 101 B), which are often short and may be reduced to a single cell (fig. 101 A). In *S. radicans* ((21) p. 231, (63)) the paired sporangia are sessile. The fertile branches mostly, if not invariably, arise from dormant branch-initials (fig. 101 J, *pe*). In species with a simple structure (e.g. *S. olivacea*) there is little distinction between them and the vegetative branches, but in those showing abundant septation (*S. plumigera*, *S. racemosa*, etc.) the fertile laterals remain comparatively simple and are not uncommonly uniseriate (fig. 101 B, *f*). Special instances are afforded by *S. bracteata* ((40) p. 253), where the fertile branches are pseudo-axillary (fig. 101 L), which is due to the fact that the first abaxial lateral (*st*) remains sterile; and by *S. Borneti* ((13) p. 38, (33) p. 15) and *S. Reinkei* ((40) p. 316), where the fertile branches are sympodial in structure and usually bear all the sporangia on the adaxial side (fig. 101 J). In *Battersia* (fig. 99 A) and *Sphacella* (fig. 92 A) the sporangia are terminal or lateral on the ordinary erect threads.

In *Chaetopteris* (fig. 101 K) formation of fertile branches is relegated to the peripheral cells of the rhizoidal cortex (cf. *Desmarestia*). These branches show quite an irregular distribution and possess a simple multiseriate structure; the sporangia are borne at the ends of few-celled laterals, but there are no other branches.

The sporangia of *Halopteris* are found in the axils of laterals of higher orders (fig. 102 C), which constitute the "bracts" of Reinke and Sauvageau; the sporangia develop from the axillary initials described on p. 274 so that on Sauvageau's interpretation they are actually terminal in position. In *H. filicina* (fig. 102 A–C) they usually occur singly on short stalks in the axils of branchlets (bracts) and replace the "axillary" laterals present on the larger axes; sometimes, however, the initial divides so that two or even four sporangia occur in the same axil. In other species (e.g. *H. funicularis* (46) p. 400) the axillary initial undergoes more plentiful division and forms a cushion of cells (fig. 102 F–L), each of which can grow out into a branched uniseriate (rarely biseriate) thread bearing a number of sporangia (fig. 102 D). A more advanced condition is seen in *H. scoparia* (fig. 102 N), in which such sori (*sp*) with their subtending "bracts" (*br*) are united into spikelets situated at the ends of the branches[1] ((46) p. 365). The lower laterals (*st*) of these spikelets are sterile and distichous, whilst the upper fertile ones (*br*) are tetrastichous. Much the same occurs in *H. hordacea*, but here the sessile sporangia are crowded together on the axillary cushions ((46) p. 426).

The fertile systems are likewise arranged in spikelets in *Phloeo-*

[1] Reinke's ((33) p. 32) *Anisocladus* was established for an alga in which all the fertile shoots arose secondarily from dormant initials. Sauvageau ((46) pp. 396, 412) has shown that this feature is inconstant and that production of sporangia on secondary shoots also occasionally occurs in *Halopteris*.

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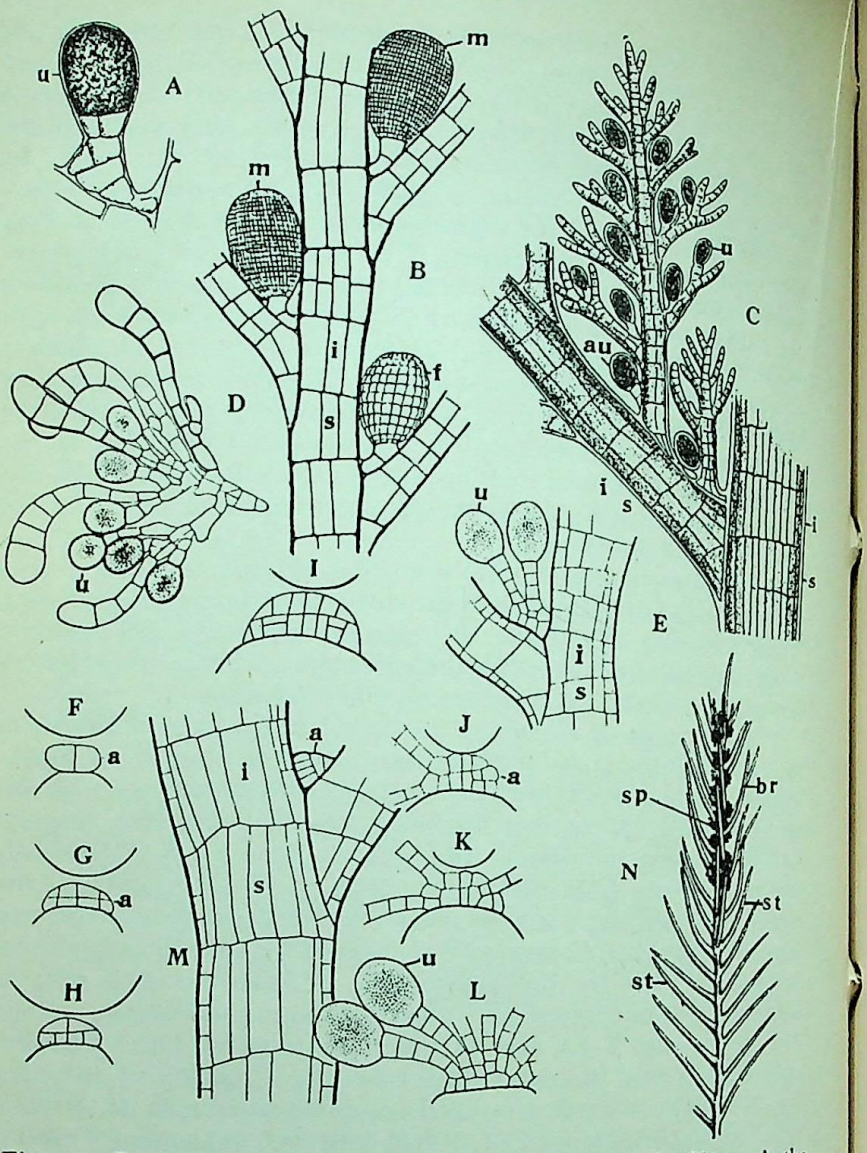

Fig. 102. Reproductive organs of *Halopteris*. A–C, *H. filicina* Kütz.; A, the pseudo-axillary unilocular sporangium; B, part of an axis, with the two kinds of plurilocular sporangia; C, reproductive branch, with unilocular sporangia. D, *H. funicularis* (Mont.) Sauv., reproductive branch with unilocular sporangia. E–N, *H. scoparia* (Kütz.) Sauv.; E, part of a longitudinal section of a fertile spike, showing axillary unilocular sporangia; F–L, successive development of an axillary cushion, in transverse section; M, young axillary cushion seen in longitudinal section; N, a fertile spike. *a*, axillary cushion; *au*, axillary unilocular sporangium; *br*, "bract"; *f*, female and *m*, male plurilocular sporangium; *i*, inferior and *s*, superior secondary segment; *sp*, sporangium; *st*, sterile lateral; *u*, unilocular sporangium. (A, C, N after Reinke; the rest after Sauvageau.)

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caulon (fig. 103 A), but here the cushions produced from the axillary initials give rise, on either side of the sorus, to a short branch (fig. 103 A–C, *br*) which occupies the position of a "bracteole" with respect to the subtending "bract" (*b*; (33) p. 30). In *P. foecundum* ((46) p. 454) additional sporangia (fig. 103 D, *au*) arise adventitiously from the peripheral cells of the axis of the spikelet.

In *Philopogon* ((33) p. 35, (46) p. 476) most of the fertile branches are again axillary (fig. 103 I, *f*), arising from large-celled cushions (*ax*), which are produced in the axils of the laterals of limited growth (*l*); these remain dormant for a considerable time and as a result become deeply embedded in the secondary cortex (*c*, cf. p. 268). When the reproductive period sets in, the cushions develop into branches which remain apposed to the subtending lateral (fig. 103 I, *f*) and at or near the surface of the cortex give rise to a tuft of threads bearing the sporangia (fig. 103 E–G). Similar fertile branches (fig. 103 I, *af*) also arise from other points on the axis, their exact mode of origin being not yet clear ((46) p. 477).

The fertile branches of *Cladostephus verticillatus* ((23*a*) p. 444, (31) p. 158, (52) pp. 490, 556; cf. also (59) p. 45), lastly, are formed successively during winter from the basal parts of the older axes, at a time when the upper portions have often largely perished (fig. 106 A). The fertile laterals ultimately constitute dense cushions (*f*), which more or less completely envelop the perennating parts. They arise from surface-cells of the secondary cortex (fig. 103 H), or of the rhizoidal cortex, and continued growth of these tissues often results in the bases of the fertile laterals (*f*) becoming embedded. The fertile branches are in general simpler than the vegetative ones, but they vary considerably in the amount of septation and the number of sporangia, as well as in the presence or absence of lateral hairs and branches, both of which are holoblastic in origin; the sporangia are borne on the superior secondary segments. The mode of origin of the fertile branches of *Cladostephus* resembles that of *Chaetopteris*.

The unilocular sporangia are generally globular or oblong in form (figs. 101 A, B, J; 102 C, D, L, *u*). At maturity the contents enclosed in a common mucilage-envelope escape through an apical aperture, the individual swarmers slowly separating from one another ((6) p. 17, (30), (31) p. 161). The plurilocular sporangia ((40) p. 217) are commonly spherical or oblong (figs. 101 C–E, K, L; 102 B) and never markedly elongate. They generally possess only two series of compartments, often surrounding a central cavity. The swarmers are either liberated individually from each loculus (*Sphacelaria* (23) p. 375; *Cladostephus*) or the septa disappear at maturity and all the contents are set free through an apical aperture (*Halopteris*, *Sphacelaria olivacea* (41) p. 59).

Proliferation of the unilocular sporangia is frequent. The stalk-cell may grow into a vegetative branch ((31) p. 170), but more usually another sporangium is formed (fig. 99 B). In *Cladostephus verti-*

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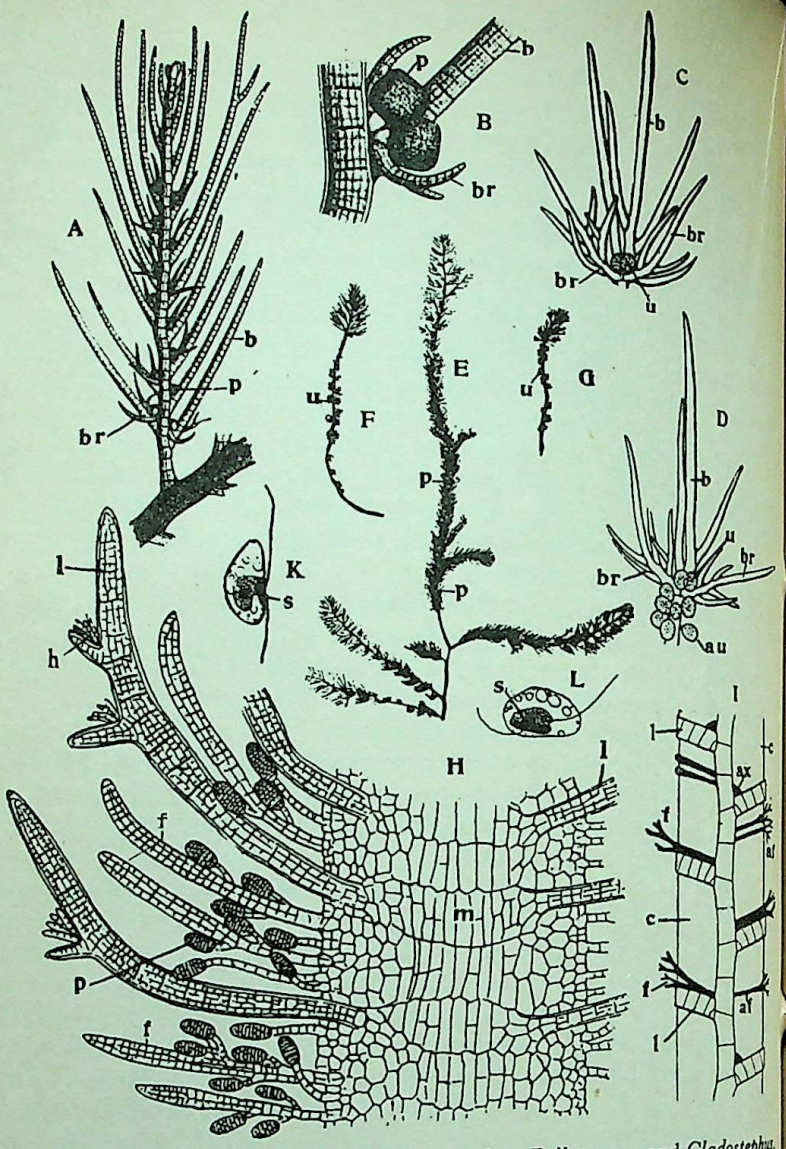

Fig. 103. Reproductive organs of *Phloeocaulon*, *Ptilopogon*, and *Cladostephus*. A, B, *Phloeocaulon spectabile* Reinke; A, fertile spike with plurilocular sporangia; B, small part of same enlarged, showing the "bracteoles" (*br*). C, D, *P. foecundum* Sauv.; C, "bract" (*b*), with the two axillary sporangia and the two "bracteoles" (*br*); D, the same, together with part of the underlying axis from which the "bracts" have been removed, showing adventitious sporangia (*au*). E–G, I, *Ptilopogon botryocladus* Reinke; E, part of a fertile plant, with adventitious branches bearing plurilocular sporangia; F, G, the same bearing unilocular sporangia; I, diagrammatic longitudinal section of a shoot of unlimited growth showing dormant axillary cushions (*ax*) and others which have grown out into fertile branches (*f*). H, *Cladostephus verticillatus* Ag., part of a long shoot in longitudinal section, with reproductive branches. K, L, *C. spongiosus* C. Ag., swarmers. *af*, accessory and *ax*, axillary fertile branches; *au*, adventitious sporangium; *b*, "bract"; *br*, "bracteole"; *c*, cortex; *f*, fertile branch; *h*, hair; *l*, lateral; *m*, medulla; *p*, plurilocular and *u*, unilocular sporangium. (C, D, I after Sauvageau; H after Pringsheim; K, L after Kuckuck; the rest after Reinke.)

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cillatus the underlying cell ((31) p. 162) bulges into the sporangium before it has discharged its contents. Except where heterogamy is suspected, there is no essential difference between the swarmers from the two types of sporangia. They possess (figs. 101 F, H; 103 L; 104 *F*) one or more chromatophores (*c*), one of which commonly bears an eye-spot (*s*). According to Kuckuck ((24) p. 178) both kinds of sporangia are usually formed during the cold season.

THE LIFE-CYCLE

The unilocular sporangia are no doubt normally organs of asexual reproduction, reduction during spore-formation having been demonstrated in *Sphacelaria bipinnata* (6), *Halopteris scoparia* (15) and *H. filicina* (28). Since plurilocular sporangia commonly occur on distinct individuals and their swarmers have been shown to behave as gametes in *Cladostephus spongiosus* (56) and *Sphacelaria bipinnata* (30), such plants must be haploid, although this has not up to the present been proved cytologically. Plurilocular sporangia may, however, also occur on the same individuals as the unilocular ones and, in *S. bipinnata* ((6) p. 17), their swarmers have been shown to be diploid, as in many Ectocarpales (cf. also (24) p. 179). The two types of sporangia are found on the same plant in several other species of *Sphacelaria* ((31) p. 170, (41), (42)), although in most of these (cf. e.g. (21) p. 232) individuals bearing plurilocular sporangia alone are also recorded, suggesting the probable existence of haploid plants. About 90% of the individuals of *S. bipinnata* examined by Papenfuss (30) bore unilocular sporangia only.

It is significant that the species of *Halopteris*, apart from *H. filicina* ((43) p. 419), never bear the two types of sporangia on the same plant. This segregation is also found in *Phloeocaulon*, *Ptilopogon*, *Chaetopteris*, and *Cladostephus*. This implies that, in the more specialised Sphacelariales, the occurrence of plurilocular sporangia (presumably always diploid) on individuals bearing the unilocular type has, as in Ectocarpales (cf. p. 131), either become exceptional or is altogether suppressed.

Fusion of the swarmers from the plurilocular sporangia has been demonstrated in *Cladostephus spongiosus*. Schreiber(56) observed abundant copulation (fig. 104 A–E) and established that there are positive and negative strains. The two types of gametes are indistinguishable, but the female (fig. 104 B, *f*) round off at an early stage and, losing their flagella, are sought out by the more active male gametes (*m*). Schreiber concludes that, in *C. spongiosus*, there is an isomorphic alternation between a sporophyte with unilocular and a gametophyte with plurilocular sporangia (gametangia). Both types of gametes can also develop apogamously ((56) p. 240). The same authority failed to obtain fusion of the swarmers from the plurilocular

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sporangia of *Chaetopteris plumosa* and therefore regards them as diploid, but it is equally possible that some factor in the cultures prevented the occurrence of sexual fusion.

In *Sphacelaria bipinnata* Clint ((6) p. 17) records the fusion of the haploid swarmers from the unilocular sporangia, although the data are not convincing and give the impression of abnormal occurrences. Papenfuss ((30) p. 443) did not observe any such fusion, although the germlings from these swarmers (fig. 104 G–I) did not develop beyond the one-celled stage; this is perhaps related to the endophytic habit of the species in question. The swarmers from the plurilocular sporangia of diploid plants likewise failed to fuse, but in plants bearing such

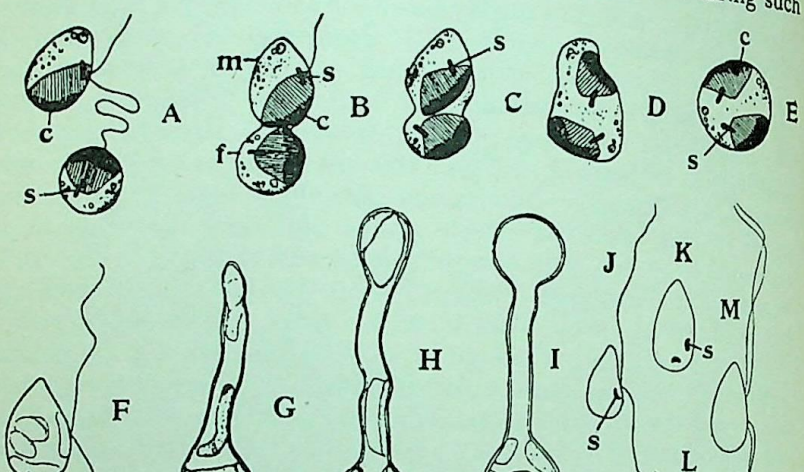

Fig. 104. A–E, *Cladostephus spongiosus* C. Ag.; A–D, sexual fusion; E, zygote. F–M, *Sphacelaria bipinnata* Sauv.; F, zoospore; G–I, stages in germination of same; J, gamete; K, L, zygotes; M, motile zygote. *c*, chromatophore; *f*, female and *m*, male gamete; *s*, stigma. (A–E after Schreiber; F–M after Papenfuss.)

sporangia only they function as gametangia. This species is monoecious, and both gametes are motile when they copulate; the two corresponding flagella of the zygote are usually wound round one another (fig. 104 M) and the product remains motile for several hours.

Swarmers from the unilocular sporangia have also been stated to copulate in *Halopteris filicina* and *H. scoparia* ((20) p. 318), although Higgins (15) failed to corroborate this in the latter species. The possibility of such fusion cannot be denied in view of its occurrence in Ectocarpales. Sauvageau (51), however, grew practically mature plants of *H. scoparia* from the swarmers of the unilocular sporangia without observing fusion, a fact which is strongly in favour of their being asexual. On the other hand, the swarmers from the plurilocular

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sporangia of *Cladostephus verticillatus* developed directly into vigorous plants ((52) p. 563; cf. also (50)), which either implies that they were diploid or that apogamous development readily occurs in this species.

The gametangia of *Cladostephus spongiosus* and *Sphacelaria bipinnata* are all of one type, and this appears to be true of several other *Sphacelarias* (e.g. *S. olivacea* ((41) p. 59). Several species of *Sphacelaria* and *Halopteris*, however, produce plurilocular sporangia of two kinds and in all of these the unilocular sporangia seem to occur on distinct individuals. In *Sphacelaria hystrix* ((39), (42) p. 339) the two types of sporangia differ in the size of their compartments (fig. 101 C–E); the swarmers of the one (fig. 101 G) are relatively large and possess several chromatophores (*c*), whilst those of the other type (fig. 101 G′) are small and colourless. Fusion has not been observed, nor has it been possible to secure germination of either kind of swarmer. It is probable that these swarmers are gametes and that the plants producing them are gametophytic. Both they and the individuals bearing unilocular sporangia produce propagules, which are, however, formed at a later stage on special threads arising from dormant initials (45). Two types of plurilocular sporangia are also known in *S. furcigera* ((1) p. 22, (41) p. 377), but here both have relatively large compartments (megasporangia and meiosporangia ?).

Sauvageau likewise records two types of plurilocular sporangia in *Halopteris filicina* ((43) p. 419), *Phloeocaulon* ((46) pp. 462, 467), and *Ptilopogon* ((46) p. 479). They differ in colour and in the size of their compartments (fig. 102 B), those of the supposed female gametangia (*f*) being twice as large as those of the supposed male (*m*). The same authority has published data that indicate a possible further differentiation in certain species of *Halopteris*. In the spikelets of a dried specimen of *H. scoparia* ((46) p. 370, (48)), he observed reproductive organs of two types, viz. (*a*) "antheridia", with a single apical aperture and containing numerous small cytoplasmic masses arranged as in a plurilocular sporangium, although septa were not recognisable, and (*b*) somewhat pyriform "oogonia", containing a single strongly contracted mass of cytoplasm. Similar structures are also believed to occur in *H. hordacea* ((46) p. 428).[1]

The observations relating to *Halopteris* and *Phloeocaulon* were made on herbarium specimens in which the reproductive organs were no doubt poorly preserved, but they cannot for this reason be dismissed as of no value, coming as they do from so reputable an investigator. They indicate with a considerable degree of probability that in many, if not in all, the species of these two genera there are two types of plurilocular sporangia. The implied existence of heterogamy is quite in conformity with the high degree of anatomical and morphological

[1] Sauvageau ((46) p. 401) regards the plurilocular sporangia found by Reinke ((33) pl. VIII, fig. 8) in *H. funicularis* as antheridia and concludes that in this species the two types of "sex organs" are borne on distinct plants.

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differentiation exhibited by the genera in question. Greater doubts may be felt as to the existence of oogonia with a single ovum in certain species of *Halopteris* (cf. also (15) p. 352), although this cannot be regarded as altogether improbable. Those who are favourably situated for the study of these species should attempt to elucidate these important problems.

THE EARLY STAGES OF DEVELOPMENT

The first stages of germination of the spores resemble those of other Phaeophyceae already considered (fig. 104 G–I). In *Sphacelarias*, provided with a discoid basal system, the latter probably develops first. In *Halopteris hordacea* ((46) p. 429) and *H. scoparia* (51) a compact parenchymatous disc (fig. 105 C, D, *d*) is formed before the erect shoots develop.

In *H. scoparia*[1] this disc generally gives rise to a single upright thread (fig. 105 C, D, *1*) having a simple multiseriate structure (fig. 105 A, B, *1*) and bearing a number of hairs (*h*), though otherwise unbranched. After some little time its growth terminates, but before this happens it produces from one of its lower segments a single lateral (fig. 105 B, *2*) which develops into a thread of the second generation. This is rather more robust and bears a number of distichous branches, as well as hairs (fig. 105 A, *2*). This second axis, in its turn, ultimately ceases to grow and produces from near its base a still more vigorous lateral of the third generation (fig. 105 A, *3*). Ultimately a fourth arises in the same way, and this (fig. 105 A, *4*) develops into the mature plant. The production of each successive generation from a basal segment of the previous one recalls the late formation of laterals from dormant branch-initials in the mature individuals of *Halopteris*.

Such a development probably occurs also in other species of *Halopteris*. In *H. filicina* ((43) p. 411), although the first-formed erect thread may develop into an adult shoot, its growth is commonly limited, the functional mature shoot then arising as a lateral branch from near its base. The first erect thread of this species soon branches and develops rhizoids from its lower cells. These envelop the part of the axis below and spread out over the substratum, where they expand into small discs which may fuse to form larger ones and which give rise to other erect axes; these may exhibit a similar development.

The small disc produced from the swarmers (fig. 106 B, C, *d*) of *Cladostephus verticillatus* ((49), (52) p. 566) always gives rise in the first place to a long hair (*h*), after which a simple erect thread of limited

[1] The gelatinous envelope of the disc is derived, according to Sauvageau ((51) p. 47), from the membrane of the spore. The small body *g* in fig. 105 C and D, which much resembles an original spore which has undergone division, is regarded by Sauvageau as a problematic outgrowth from the disc.

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growth (fig. 106 B–D, *1*) is formed. Subsequently other more robust axes develop from surface-cells of the enlarging disc (fig. 106 D, *2–4*), but it is only after a number of these have been formed that there

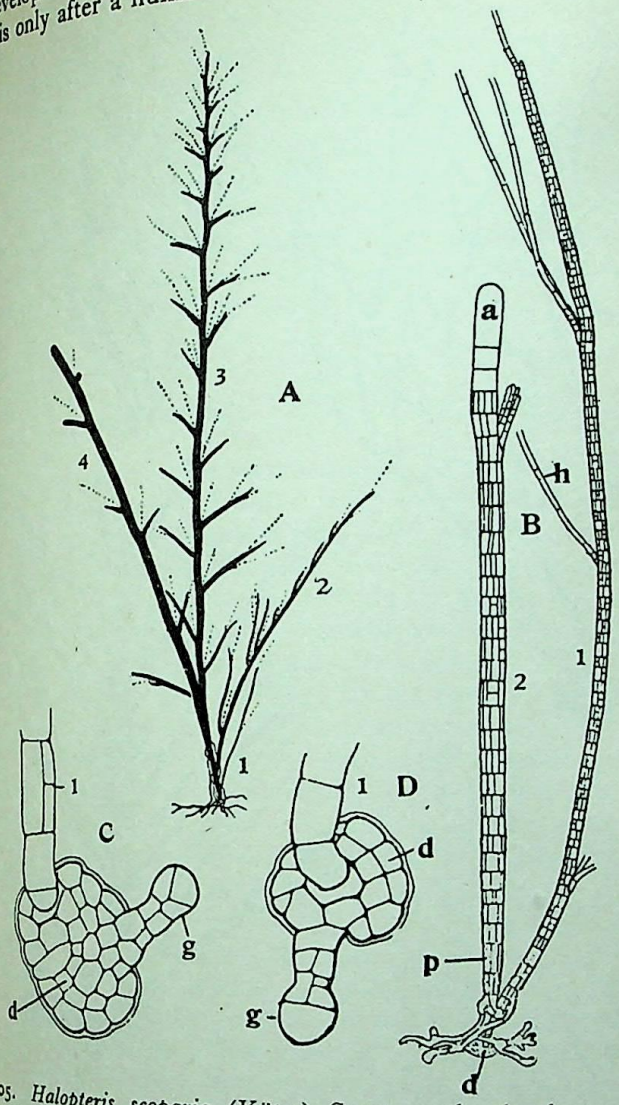

Fig. 105. *Halopteris scoparia* (Kütz.) Sauv., early development (after Sauvageau). A, diagram of development, the dotted lines representing hairs, 1–4 the successively developing axes; B, development of second axis (2) from base of primary one (1); C, D, early stages, showing embryonic disc (*d*) and base of primary axis (1). *a*, apical cell; *d*, basal system; *g*, body of doubtful nature; *h*, hair; *p*, pericyst.

arises a shoot of unlimited growth (*5*) which develops the characteristic whorled branching and other features of the mature axis. The successive primary shoots are all of limited growth and show in-

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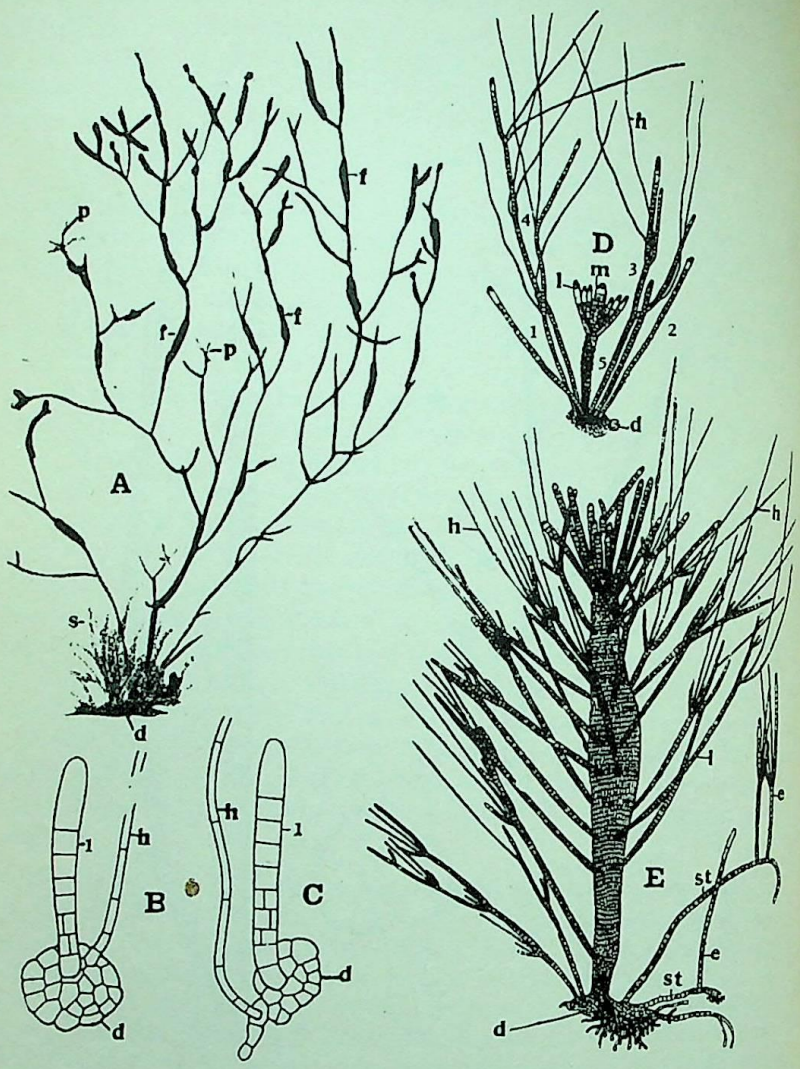

Fig. 106. *Cladostephus verticillatus* Ag. (after Sauvageau). A, part of a fertile plant in which the long shoots have shed the laterals of unlimited growth; some of the truncated ends are proliferating (*p*), while numerous new shoots (*s*) are arising from the basal disc (*d*). B, C, early stages in development. D, a much later stage, showing commencing development of the mature shoot (*m*), 1–5 the successively formed axes. E, still later stage showing further development of the mature shoot and formation of stolons (*st*) from the basal disc. *d*, basal disc; *e*, erect shoots; *f*, fertile tracts; *h*, hairs; *l*, lateral.

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creasing complexity. In the first many of the lower secondary segments do not undergo longitudinal division, but in the later ones such segmentation occurs more regularly. The first-formed shoot often bears solitary hairs only, while the subsequent ones (fig. 106 D) produce geminate hairs and show occasional holoblastic branching with axillary hairs.

Further complication is introduced by the production, from certain cells of the disc, of curved stolons (fig. 106 E, *st*) which are homologous with the upright shoots. They spread in all directions over the substratum, developing occasional coralloid haptera, especially near the bases of the upright axes that originate from the stolons. Other stolons, as already mentioned (p. 282), arise as prolongations of some of the radial files of cells composing the disc.

THE GENUS *CHORISTOCARPUS*

Choristocarpus tenellus (*Ectocarpus tenellus* Kütz.) ((10) p. 65, (22), (25) p. 13, (53) p. 158, (65) p. 1), found in deep water in the Mediterranean, is a small form with uniseriate filaments (fig. 107 A) exhibiting well-marked apical growth and alternate branching. The segments of the apical cell undergo no further appreciable elongation (fig. 107 B). The thin-walled cells contain numerous rounded or oblong chromatophores which are without pyrenoids; they are densely packed in the apical cells, but less closely in the others (fig. 107 B) so that the elongate cells present a rather characteristic transparent appearance.

The approximation to one of the simpler Sphacelariales is increased by the abundant production of propagules ((14), (22) p. 310), although these do not possess the characteristic shape of those of *Sphacelaria*. They are oblong structures borne on a unicellular stalk (fig. 107 A, *p*) and usually composed of two cells (fig. 107 D), although sometimes undivided or three-celled. Each cell is uninucleate and has alveolar cytoplasm; in the nature of the cell-contents there is much resemblance to the monospores of Tilopteridales (p. 156). After detachment of the propagule the stalk can produce a second.

Plants bearing such propagules also produce sessile unilocular sporangia occupying the same position as the former (fig. 107 A, *u*) and producing about 16 swarmers delimited by mucilage-septa (fig. 107 E). The swarmers ((25) p. 13), which are set free by an apical rupture of the sporangium, are large and move slowly; they possess numerous chromatophores, with an eye-spot next to the point of attachment of the flagella (fig. 107 F). Mature plants bearing propagules have been grown from these swarmers. Other individuals, apparently devoid of propagules, bear plurilocular sporangia (fig. 107 C) which are likewise sessile and spherical or oblong in shape ((22) p. 314). The fate of the contents is unknown.

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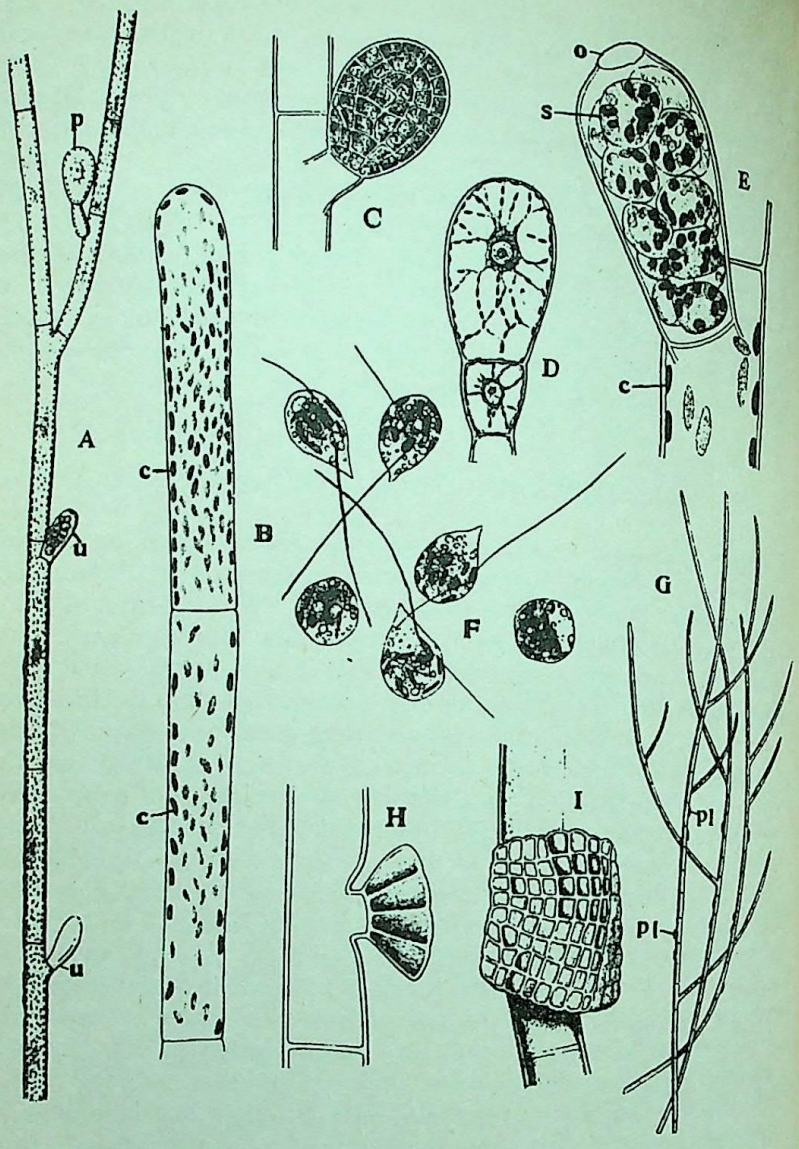

Fig. 107. A–F, *Choristocarpus tenellus* (Kütz.) Zanard.; A, part of a thread, with a propagule and two unilocular sporangia, the lower dehisced; B, apex of a thread; C, plurilocular sporangium; D, propagule; E, unilocular sporangium; F, swarmers from same. G–I, *Discosporangium mesarthrocarpum* (Menegh.) Hauck; G, threads with plurilocular sporangia; H, I, the same enlarged, H in optical longitudinal section, I from the surface. *c*, chromatophore; *o*, aperture of unilocular sporangium; *p*, propagule; *pl*, plurilocular and *u*, unilocular sporangium; *s*, swarmer. (G–I after Falkenberg; the rest after Kuckuck.)

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Kjellman ((19) p. 190) placed the rare alga *Discosporangium* (10), only once found in the Bay of Naples, together with *Choristocarpus* in a family Choristocarpaceae. Falkenberg had already emphasised the general resemblances in vegetative characters, although the branches in *Discosporangium* arise from the middle of the parent-cell (fig. 107 G). The sole reproductive organs, so far observed, are plurilocular sporangia which form a one-layered plate around the middle of the elongate vegetative cells (fig. 107 G–I); in some ways they recall those of *Zosterocarpus* (p. 55).

The systematic position of *Discosporangium* remains altogether obscure. The apical growth and other features suggest an affinity with *Choristocarpus*, but the reproductive organs scarcely lend support for such a relationship ((22) p. 317, (25)). Schmidt (55) contributes nothing.

THE AFFINITIES AND STATUS OF THE SPHACELARIALES

In their pronounced apical growth and characteristic segmentation the Sphacelariales form a clearly defined group which is almost certainly a natural one. The numerous modifications that occur are all traceable to a common plan and warrant the assumption of an ancestry among simple filamentous types with apical growth.[1] Such a type is furnished by *Choristocarpus*, which Kylin ((26) p. 306) refers to Sphacelariales, a point of view with which one may well concur. Apart from the resemblance in mode of growth and cell-structure, the occurrence of propagules in *Choristocarpus* serves to emphasise the affinity. Kuckuck ((22) p. 316) drew attention to the marked similarity between the young propagules of *Sphacelaria tribuloides* and those of *Choristocarpus*. The greater degree of elaboration of the mature propagules of *Sphacelaria* has perhaps gone hand in hand with the differentiation of the vegetative system. There is much similarity, too, between *Choristocarpus* and *Sphacella*. In the latter the simple structure is possibly a result of reduction and, without further investigation, it is impossible to say whether this may not also be true of *Choristocarpus*. Be that as it may, both genera exemplify little-differentiated forms which, except in their apical growth, are not readily separated from the simpler Ectocarpales.

It has been pointed out above that in many, if not in all, Sphacelariales the life-cycle probably involves an isomorphic alternation between asexual and sexual individuals; in this respect the Sphacelariales contrast markedly with the polystichous Ectocarpales. The type of alternation also directs attention to forms like the simpler isomorphic Ectocarpaceae for the origin of the members of this order. They probably represent one of the numerous lines of evolution arising from simple filamentous Brown Algae, *Choristocarpus* being possibly an offshoot from this line (cf. also (67) p. 76).

[1] In this connection see also the genus *Acrocytis* of Rosenvinge ((38) p. 8).

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An affinity between Sphacelariales and Tilopteridales has also been suggested ((52*a*) p. 65, (57)), the monospores of the latter being regarded as equivalent to the propagules of the former. Despite certain resemblances, the importance of which it is difficult to evaluate in the present state of our knowledge, the Tilopteridales appear to be widely removed from the Sphacelariales by their intercalary (trichothallic) growth and by the fact that the monospores, whatever be their function, are of the nature of spores, since they are formed within definite sporangia.

Oltmanns, largely on the basis of Sauvageau's investigations, subdivides the order into:

1. *Sphacelariaceae:* Battersia, Chaetopteris, Disphacella, Sphacella, Sphacelaria.
2. *Stypocaulaceae:* Alethocladus, Halopteris (incl. Stypocaulon), Phloeocaulon, Ptilopogon.
3. *Cladostephaceae:* Cladostephus.

To these may be added:

4. *Choristocarpaceae:* Choristocarpus.

Literature of Sphacelariales

1. See No. 14 on p. 140 (Askenasy, 1889). **1*a*.** See No. 24 on p. 141 (Batters, 1897). **2.** See No. 32 on p. 141 (Boergesen, 1914). **3.** See No. 36 on p. 141 (Boergesen, 1939). **4.** Chemin, E. 'Sur le parasitisme de *Sphacelaria bipinnata* Sauvageau.' *C.R. Acad. Sci. Paris*, 174, 244–7, 1922. **5.** See No. 102 on p. 749 (Chemin, 1923). **6.** Clint, H. B. 'The life history and cytology of *Sphacelaria bipinnata* Sauv.' *Publ. Hartley Bot. Lab. Liverpool*, 3, 1927. **7.** Collins, F. S. & Hervey, A. B. 'The Algae of Bermuda.' *Proc. Amer. Acad. Arts and Sci.* 53, 1–195, 1917. **8.** Dickinson, C. I. 'Some marine algal balls from Tasmania.' *Ann. Bot.* 47, 253–9, 1933. **9.** See No. 54 on p. 44 (Escoyez, 1908). **10.** Falkenberg, P. 'Ueber *Discosporangium*, ein neues Phaeosporeen-Genus.' *Mitt. Zool. Stat. Neapel*, 1, 54–66, 1879. **11.** See No. 36 on p. 14 (Farlow, 1881). **12.** Geyler, T. 'Zur Kenntnis der Sphacelarien.' *Jahrb. wiss. Bot.* 4, 479–535, 1865–6. **13.** Hariot, P. 'Algues.' *Mission scient. du Cap Horn*, 1882–3, Paris, 5, Bot., 3–109, 1888. **14.** Hauck, F. '*Choristocarpus tenellus* (Kütz.) Zanard.' *Hedwigia*, 26, 122–4, 1887. **15.** Higgins, E. M. 'A cytological investigation of *Stypocaulon scoparium* (L.) Kütz., with especial reference to the unilocular sporangia.' *Ann. Bot.* 45, 345–53, 1931. **16.** Janczewski, E. 'Les propagules du *Sphacelaria cirrhosa*.' *Mém. Soc. Sci. Nat. Cherbourg*, 16, 337–44, 1871–2. **17.** Janczewski, E. 'Études anatomiques sur les *Porphyra* et sur les propagules du *Sphacelaria cirrosa*.' *Ann. Sci. Nat., Bot.* v, 17, 241–60, 1873. **18.** See No. 75 on p. 256 (Jónsson, 1904). **19.** See No. 121 on p. 143 (Kjellman, 1897). **20.** See No. 127 on p. 143 (Knight, 1929). **21.** See No. 133 on p. 143 (Kuckuck, 1894). **22.** Kuckuck, P. 'Ueber Schwärmsporenbildung bei den Tilopterideen und über *Choristocarpus tenellus* (Kütz.) Zan.' *Jahrb. wiss. Bot.* 28, 290–322, 1895. **23.** See No. 134 on p. 143 (Kuckuck, 1896). **23*a*.** See No. 16 on p. 191 (Kuckuck, 1897). **24.** See No. 145 on p. 144 (Kuckuck, 1912). **25.** See No. 147 on p. 144 (Kuckuck, 1929). **26.** See No. 15 on p. 157 (Kylin, 1917). **27.** Magnus, P. 'Zur Morphologie der Sphacelarien, etc.' *Festschr. Feier 100-jähr. Bestehens Ges. Naturf. Freunde, Berlin*, 129–56, 1873. **28.** Mathias, W. T.

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Halopteris filicina Kütz. The cytology of the reproductive organs.' *Publ. Hartley Bot. Lab. Liverpool*, 13, 25–8, 1935. **29.** See No. 182 on p. 145 (Olmanns, 1922). **30.** PAPENFUSS, G. F. 'Alternation of generations in *Sphacelaria bipinnata* Sauv.' *Bot. Notiser*, 437–44, 1934. **31.** PRINGSHEIM, N. 'Ueber den Gang der morphologischen Differenzierung in der Sphacelarien-Reihe.' *Abh. Akad. Wiss. Berlin, Phys. Kl.* 137–91, 1873 (Gesammelte Abhandl., 1, 359–414, 1895). **32.** See No. 198 on p. 145 (Reinke, 1889). **33.** REINKE, J. 'Beiträge zur vergleichenden Anatomie und Morphologie der Sphacelariaceen.' *Bibl. Bot.* 23, 1891 (see also *Ber. Deutsch. Bot. Ges.* 8, 201–15, 1890). **34.** REINKE, J. 'Ueber Gäste der Ostseeflora.' *Ibid.* 10, 4–12, 1892. **35.** See No. 200 on p. 145 (Reinke, 1892). **36.** See No. 202 on p. 145 (Rosenvinge, 1893). **37.** See No. 203 on p. 145 (Rosenvinge, 1899). **38.** ROSENVINGE, L. K. 'Marine Algae from Kangordlugssuak.' *Meddelels. om Grønland*, 104, No. 8, 1933. **39.** SAUVAGEAU, C. 'Sur la sexualité et les affinités des Sphacélariacées.' *C.R. Acad. Sci. Paris*, 126, 1672–5, 1898. **40.** SAUVAGEAU, C. 'Remarques sur les Sphacélariacées.' *Journ. de Bot.* 14, 213 et seq., 1900. **41.** SAUVAGEAU, C. 'Remarques sur les Sphacélariacées.' *Ibid.* 15, 22 et seq., 1901. **42.** SAUVAGEAU, C. 'Remarques sur les Sphacélariacées.' *Ibid.* 16, 325 et seq., 1902. **43.** SAUVAGEAU, C. 'Remarques sur les Sphacélariacées.' *Ibid.* 17, 45 et seq., 1903. **44.** SAUVAGEAU, C. 'Sur les *Sphacelaria* d'Australasie.' *Notes Bot. School, Trinity Coll. Dublin*, 1, 196–200, 1902. **45.** SAUVAGEAU, C. 'Sur les variations du *Sphacelaria cirrhosa* et sur les espèces de son groupe.' *Mém. Soc. Sci. Phys. Nat. Bordeaux*, VI, 3, 309–19, 1903. **46.** SAUVAGEAU, C. 'Remarques sur les Sphacélariacées.' Fasc. 2, Paris, 337–480, 1904 (pp. 337–48 in *Journ. de Bot.* 18, 88–104, 1904). **47.** SAUVAGEAU, C. 'Sur les pousses indéfinies dressées du *Cladostephus verticillatus*.' *Act. Soc. Linn. Bordeaux*, 61, 69–94, 1906. **48.** SAUVAGEAU, C. 'Sur la sexualité de l'*Halopteris* (*Stypocaulon*) *scoparia*.' *C.R. Soc. Biol. Paris*, 62, 506–7, 1907. **49.** SAUVAGEAU, C. 'Sur la germination et les affinités des *Cladostephus*.' *Ibid.* 62, 921–2, 1907. **50.** SAUVAGEAU, C. 'Nouvelles observations sur la germination du *Cladostephus verticillatus*.' *Ibid.* 64, 695–7, 1908. **51.** SAUVAGEAU, C. 'Sur le développement échelonné de l'*Halopteris* (*Stypocaulon* Kütz.) *scoparia* Sauv. et remarques sur le *Sphacelaria radicans* Harv.' *Journ. de Bot.* 11, 2, 44–71, 1909 (see also *C.R. Soc. Biol. Paris*, 65, 162–3, 1908). **52.** SAUVAGEAU, C. *Remarques sur les Sphacélariacées*. Fasc. 3, Bordeaux, 481–628, 1914. **52*a*.** See No. 23 on p. 157 (Sauvageau, 1928). **53.** See No. 240 on p. 146 (Sauvageau, 1931). **54.** SCHINGNITZ VON BÖSELAGER, A. 'Beiträge zur Kenntnis der *Sphacelaria cirrosa*.' *Hedwigia*, 75, 285–90, 1936. **55.** SCHMIDT, O. C. 'Choristocarpaceen und Discosporangiaceen.' *Ibid.* 77, 1–4, 1937. **56.** SCHREIBER, E. 'Ueber die geschlechtliche Fortpflanzung der Sphacelariales.' *Ber. Deutsch. Bot. Ges.* 49, 235–40, 1931. **57.** See No. 26 on p. 157 (Schussnig, 1928). **58.** See No. 179 on p. 259 (Skottsberg, 1907). **59.** See No. 180 on p. 259 (Skottsberg, 1921). **60.** See No. 234 on p. 48 (Swingle, 1897). **61.** See No. 277 on p. 147 (Taylor, 1928). **62.** See No. 279 on p. 147 (Taylor, 1937). **63.** TRAILL, G. W. 'On the fructification of *Sphacelaria radicans* Harvey and *S. olivacea* J. Ag.' *Trans. Bot. Soc. Edinburgh*, 17, 77–8, 1888. **64.** WITTROCK, V. B. 'Ueber *Sphacelaria cirrhosa* (Roth) Ag., *β aegagropila* Ag.' *Bot. Centralbl.* 18, 283–4, 1884. See No. 19 on p. 180 (Zanardini, 1860). **66.** ZIMMERMANN, W. 'Zytologische Untersuchungen an *Sphacelaria fusca* Ag., etc.' *Zeitschr. Bot.* 15, 113–75, 1923. **67.** See No. 312 on p. 396 (Fritsch, 1943).

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Order VIII. *DICTYOTALES*

The genera classed in this order form a natural group, distinguished not only by the apical growth, the usual dichotomous branching in one plane (figs. 108 A; 110 A, B, G), and the lack of anatomical differentiation of the foliose thalli, but also by the oogamous sexual reproduction and the probable occurrence of isomorphic alternation in all the members. The asexual phase bears sporangia (fig. 108 G, *sp*) which produce large motionless spores, commonly in fours (*tetraspores*), though other numbers sometimes occur. The antheridia and oogonia of the sexual phase are commonly grouped in well-defined sori (fig. 112 A, B), and the single ovum is, as usual in Phaeophyceae, liberated prior to fertilisation. The antheridia (fig. 112 F) resemble the plurilocular sporangia of other orders and produce numerous minute colourless spermatozoids (fig. 112 C). There are no evident affinities with other specialised Phaeophyceae exhibiting apical growth, and the nearest relatives must be sought among the less highly differentiated forms. The Dictyotales, like the Sphacelariales, have probably originated from simple filamentous types with an isomorphic life-cycle, although evolution has here followed a different course. Most of the non-European genera are imperfectly known.

The Dictyotales are for the most part inhabitants of warmer seas (cf. e.g. (24) p. 101, (57) p. 116, (73) p. 507). The three largest genera —*Dictyota*, *Padina*, and *Dictyopteris* (*Neurocarpus*, *Halyseris*)—are practically world-wide in their distribution, but, except for the first with two, each is represented only by a single species on North European shores. The northern part of North America, both on the Atlantic and Pacific coasts, is practically destitute of representatives of this order ((19), (55) p. 168, (56) p. 650, (58)). The considerable genus *Zonaria* is widely distributed in warmer regions, a common tropical species being *Z. variegata*; several species are recorded from New Zealand ((26) p. 218), although none occur in North Temperate regions. *Taonia atomaria* is found over a large part of Northern Europe and is known from the Canary Isles and the Mediterranean. The Dictyotales, especially species of *Zonaria*, are well represented in the Southern Hemisphere, and the remarkable genus *Lobospira* is so far only recorded from Australia.

Most Dictyotales grow in permanently submerged situations and the normal habitat is probably in water of some depth. Certain species (*Dictyota dichotoma*, *Padina pavonia*) are, however, commonly found in rock-pools between tide-levels and it is evident that various Dictyotales can exist in a variety of situations (cf. also ((20) p. 252).

VEGETATIVE STRUCTURE

Dictyota dichotoma ((15), (44) p. 184, (47) p. 3, (59) p. 7), the commonest British representative, is a widely distributed annual. The familiar forked fronds (fig. 108 A), all the branches of which are normally

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situated in the same plane, arise from a cylindrical rhizome attached to the substratum by tufts of sometimes branched rhizoids. These can also develop from cells of the flat thallus, which is sometimes partly prostrate and attached. The lower part of the erect fronds is likewise

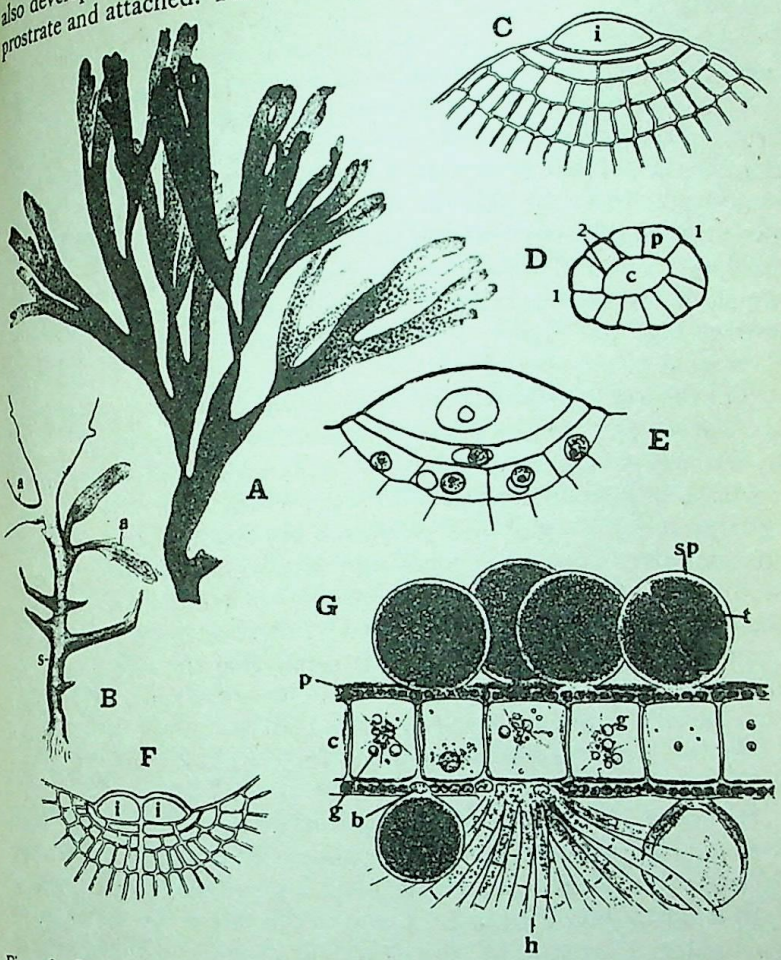

Fig. 108. *Dictyota dichotoma* (Huds.) Lamour. A, habit; B, basal part of a plant showing adventitious branches; C, apex of thallus in surface-view; D, segment of thallus in transverse section, *1*, *2* the first division-walls; E, apical cell and segmentation; F, dichotomy; G, section of thallus bearing tetrasporangia (*t*). *a*, adventitious branch; *b*, basal cell of sporangium; *c*, central cell of thallus; *g*, refractive globules; *h*, hair; *i*, apical cell; *p*, peripheral layer of thallus; *s*, cylindrical basal part of thallus; *sp*, sporangium. (A, G after Thuret; B after Reinke; C, F after Cohn; D, E after Wenderoth.)

cylindrical (fig. 108 B, *s*) and commonly gives rise to adventitious laterals (*a*), some of which may develop as horizontal stolons ((47) p. 4).[1]

[1] It is not altogether clear whether the erect fronds are lateral branches of the rhizome or, as is perhaps more probable from analogy with *Padina*, represent its upturned ends.

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Both the lower cylindrical parts and the flattened fronds, into which they gradually expand (fig. 108 B), grow by means of a single lenticular apical cell (fig. 108 C, *i*) which, when viewed from above, appears circular in the cylindrical and elliptical in the flattened portions. On the broader fronds the apical cell is often slightly sunk (cf. fig. 108 F), but when the thallus is more finely divided (var. *implexa*) the segments gradually narrow to the apical cell.

The latter cuts off a single series of segments (fig. 108 C, E) which broaden considerably behind the apex (44) and undergo regular segmentation. In the flat thallus the first curved wall (fig. 108 D, *1*) runs approximately parallel to the plane of flattening and divides the segment into two unequal cells (64). The second wall (*2*) arises in the same plane in the larger cell and separates a central (*c*) from two peripheral cells, which divide by consecutive longitudinal walls perpendicular to the surface (fig. 108 C, E); this is accompanied by some vertical segmentation of the central cell.

The mature thallus thus comes to consist of three layers (fig. 108 G), a middle one (*c*) of large cells with few or no chromatophores bounded by layers (*p*) of small cells, densely packed with chromatophores. The central cells contain, apart from fucosan-vesicles, conspicuous groups of large refractive globules (*g*) which are suspended by cytoplasmic strands; they appear to constitute some kind of food-reserve (fat according to Hansen ((23) p. 268) and are stated to be responsible for the iridescence commonly exhibited by this alga ((6) p. 708, (12) p. 162, (35) p. 73). The rather thick walls separating the cells possess conspicuous pits (fig. 112 B, *pi*). Tufts of colourless hairs, with the usual basal meristem, are scattered over both surfaces of the thallus (fig. 108 G, *h*), but are shed during the reproductive phase. In the cylindrical thallus there are from 3 to 6 layers of internal cells.

Dichotomy is effected by longitudinal division of the apical cell into two equal halves (fig. 108 F), the classical instance of such branching. Adventitious laterals, which develop from single marginal cells ((47) p. 6) and expand in the same plane as the rest of the thallus, are not uncommon; they tend to arise especially at points of injury and, after death of the parent, become independent and constitute a prolific source of vegetative reproduction. According to Schreiber ((54) p. 269) pieces of the thallus provided with an apical cell readily develop into new plants.

In other species of *Dictyota* ((4) p. 45) the dichotomy is commonly not so regular and, as a result of more vigorous development of the one limb, a pinnate habit (e.g. *D. Binghamiae* J. Ag.) may be realised. In certain species the fronds are toothed (e.g. *D. ciliata* J. Ag.). The flat thalli sometimes possess two or more layers of central cells and species exhibiting this feature have been referred to a separate genus *Dilophus* ((3) p. 106, (4) p. 84), but the maintenance of such a distinction presents considerable difficulties (cf. (56) p. 651).

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Padina pavonia ((4) p. 31, (7), (44) p. 180, (47) p. 15) is a rare perennial found near mid-tide level on the southern shores of England, but it is abundant in the Mediterranean and other warmer seas, where the majority of the other species occur. The numerous stalked fan-shaped fronds (cf. fig. 109 A), 5–12 cm. high, the larger ones often loosely rolled on their longitudinal axis like a cornet, are distinctive of all the species of the genus. The stalk of each frond is the upward continuation of a branch of the prostrate perennial rhizome (fig. 109 C, *rh*), which is richly branched and attached to the substratum by tufts of rhizoids (*r*). The stalks of the fans bear a considerable number of laterals (*l*), which are terete at the base but flatten somewhat at their summit. Many of them do not develop beyond this stage, but some may widen out and form secondary fans, the stalks of which produce other fronds in the same manner. In this way extensive branch-systems may arise. Except for the distinctive shape of the fronds, the morphology of *Padina* recalls that of *Dictyota*.[1]

The concentric zones on the fans are due to hairs (fig. 109 B, *sp*), which are arranged in 4–8 rows. The zones of hairs occur alternately on the two surfaces, but are more strongly developed on the upper and are stated to be ((7) p. 262) specially prominent in plants exposed to strong light. The reproductive organs are formed on either side of these zones, although during their development the hairs are shed. There is often a thin incrustation of carbonate of lime, especially on the upper surface; as a result the fronds appear whitish, although olive-green or reddish hues are also frequent.

The cylindrical shoots possess a single apical cell like that of *Dictyota* (cf. fig. 109 I); the segments divide into a central and four peripheral cells, all of which undergo further segmentation. The young flabellate fronds also grow by means of a single apical cell, but the mature fans possess a marginal meristem (fig. 109 F).

When a young frond is about to develop into a fan ((44) p. 180, (46) p. 443, (47) p. 17), the segments of the apical cell (fig. 109 F, *1*, *2*) undergo copious longitudinal division so that there is rapid broadening behind the apex; as a result the angle formed by the two edges of the thallus becomes more and more obtuse until it approaches 180°. The apical cell (*a*), flanked by later-formed segments (*3*, *4*, *5*), now appears in the middle of the broad front margin, while the outer cells (fig. 109 F, *i*), produced by longitudinal division of the older segments, are situated

[1] Collins ((16) p. 251) described a sterile alga (*Dictyerpa*), which was found washed up on the shores of Jamaica and appeared like "rolled and twisted strings, up to 20 cm. long" and 1–3 mm. thick. The terete strands showed dichotomous or trichotomous branching, with occasional irregularly disposed laterals, each branch being capped by a hemispherical apical cell and traversed internally by a single row of cylindrical cells. This may prove to be the rhizome of some member of Dictyotales, although Svedelius ((38) p. 188) suggests that it may be an unattached form of *Dictyota*, comparable to those known among Fucales and like them sterile (cf. also (10) p. 444).

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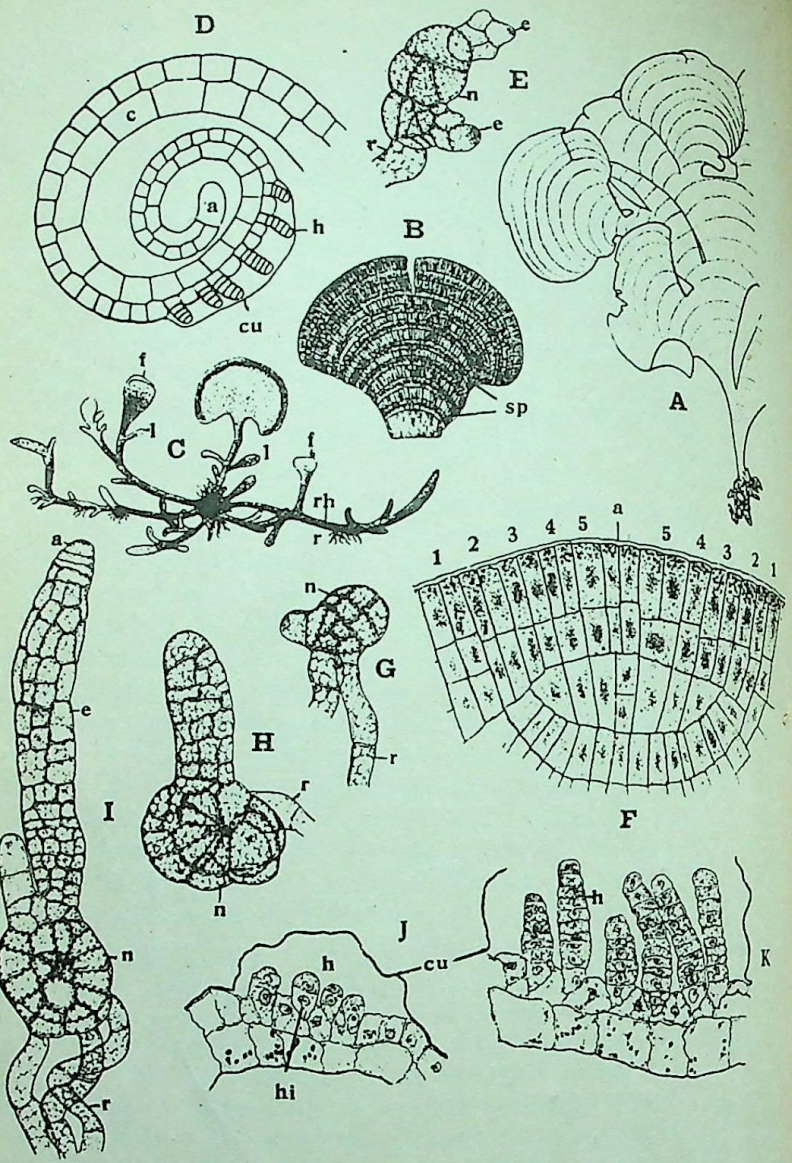

Fig. 109. *Padina*; A, *P. Vickersiae* Hoyt; B, *P. gymnospora* (Kütz.) Vickers; D, *P. Sanctae Crucis* Boerges.; C, F–K, *P. pavonia* (L.) Gaill. A, habit; B, part of thallus showing hairs and sporangia (*sp*); C, developing plant; D, longitudinal section through margin of a fan; E, G–I, germlings of tetraspores; F, surface-view of margin of developing fan, showing position of original apical cell (*a*) and marginal initials, 1–5 segments of the apical cell; J, K, development of hairs, longitudinal sections. *a*, apical cell; *c*, central cell of thallus; *cu*, cuticle; *e*, erect shoots; *f*, fan; *h*, hair; *hi*, hair-initial; *i*, initials; *l*, lateral; *n*, nodule; *r*, rhizoid; *rh*, rhizome. (A after Taylor; B, D after Boergesen; C, F after Reinke; E, G–K after Carter.)

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almost on a level with it. All the cells at the front edge acquire dense cytoplasmic contents and become meristematic; they lengthen perpendicular to the margin and undergo repeated periclinal division, accompanied by some anticlinal division, whereby the number of files of cells is increased. The original apical cell (*a* in fig. 109 F) either divides longitudinally or perishes, its place being taken by cells of the underlying segment. The semicircular edge of the enlarging fan is now occupied by an extensive series of marginal initials which have the shape of bricks placed edgewise, with their greatest width perpendicular to the surface of the thallus.

The segments cut off from the cells of the marginal meristem (fig. 109 D) soon divide longitudinally into two somewhat unequal parts, the smaller segment lying towards the morphologically upper side.[1] As a consequence of more rapid elongation of these upper segments, the free edge of the fan becomes circinnately inrolled towards the lower side ((44) p. 181, (47) p. 20), a feature which is specially obvious in longitudinal sections (fig. 109 D); illumination of the fans from below causes disappearance of the inrolling, which may even set in in the reverse direction ((7) p. 258). The lower layer of small peripheral cells (fig. 111 F) is generally cut off only at a considerable distance behind the apical meristem. In *P. Sanctae Crucis* ((9) p. 201), in fact, the two-layered condition persists throughout the plant. Both in *P. pavonia* and other species the middle layer of cells may later undergo further division parallel to the surface.

The hairs commence to develop in the inrolled part near the apex ((47) p. 21) and, according to Carter ((13) p. 142), arise from cells distinguished by their dense cytoplasm and large nuclei. These cells cut off the small hair-initial (fig. 109 J, *hi*) by an oblique wall, usually on their distal side; the initial then divides transversely to form the hair (fig. 109 K), which later develops a basal meristem. The group of hairs is at first covered by the common cuticle (*cu*), which ruptures sooner or later. Bitter ((7) p. 265) deals with response of the thalli to various types of wounding.

In general habit *Taonia atomaria* (*Dictyota atomaria* Grev. (1) p. 101, (4) p. 24, (27) pl. 1, (47) p. 26) resembles a robust *Dictyota*, the wedge-shaped segments having irregularly toothed margins (fig. 110 I). As in *Padina*, there are transverse zones of hairs forming zigzag bands (*h*), alternating on the two surfaces of the thallus. The fronds, which may reach a length of 30 cm., show repeated di- or polychotomous branching in one plane. They arise singly or in tufts from a dense felt of septate rhizoids which are produced in large numbers from the lower cells ((47) p. 26) and spread out to form a false attaching disc. According to Robinson ((50) p. 114) new fronds can develop from these rhizoids.

[1] Bitter (7) uses the terms upper and lower in the opposite sense to Reinke.

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The young frond possesses a single apical cell, but this rapidly gives place to a marginal meristem occupying the almost straight front edge; its cells, as in *Padina* and *Zonaria*, are widest at right angles to the surface. Branching is due to cessation of division in one of the initials. According to Reinke the marginal teeth are formed by the segmentation of special wedge-shaped initials. The mature thallus is six-layered, the superficial cells being rather larger than in the genera previously considered ((23) p. 274). The occasional adventitious branches probably arise from surface-cells.

Closely related to the two genera just considered is *Zonaria*[1] ((2), (3) p. 120, (28), (52)). The branched, usually erect fronds (fig. 110 A, B) show transverse zones of hairs (*h*), which are generally more abundant on one surface than on the other. The method of attachment is as in *Taonia*, the basal weft of rhizoids often attaining considerable thickness and in diverse species forming a kind of pseudo-parenchymatous stalk supporting the rest of the plant ((28) p. 241, (52) p. 67). In Z. *flava* (Clem.) Ag. ((52) p. 70) new fronds can develop from the rhizoids. *Zonaria* and *Taonia* thus do not possess the rhizomatous attachment-system found in *Dictyota* and *Padina*.

A more aberrant form is constituted by *Zonaria variegata* Lamour. ((9) p. 197, (11) p. 91, (49), (52) p. 73), the young thallus of which is often completely prostrate, forming an expanse, 1–10 cm. wide, resembling an *Aglaozonia* and attached by numerous rhizoids. A number of thalli commonly grow over one another and become fused. The older thalli are erect and it appears that growth may be erect from the first.[2]

The growth and branching of the *Zonaria*-thallus (fig. 110 H) takes place in the same way as in *Taonia*. The segments (fig. 110 D, *s*) of the diverse initials (*i*) ((28) p. 242, (49) p. 87) divide into superficial and central cells (*c*); the latter give rise to a number of layers, while the former divide by vertical walls so that the cells composing the thallus lie in regular vertical rows. In *Z. Farlowii* the surface-cells along the median line of the thallus produce adventitious branches (fig. 110 F, *b*) which develop rhizoids at their base and readily become detached ((28) p. 251). *Z. flava* is stated to show iridescence ((20) p. 238).

Padina, *Taonia*, and *Zonaria* show many points of similarity and no doubt constitute a closely allied group. A more distinctive type is furnished by *Dictyopteris* (*Halyseris* (4) p. 42). *D. membranacea* (Stackh.) Batt. (*D. polypodioides* Lamour. (27) pl. 19), a rare sublittoral

[1] Several species of *Zonaria* have been referred to distinct genera (*Stypopodium*, *Gymnosurus* (4) p. 9), but these scarcely appear well founded ((52), p. 72; cf. however (63*a*) p. 177).

[2] Sauvageau ((52) p. 79) suggests that the *Z. parvula* of Reinke ((47) p. 34), which is entirely prostrate, may be a young stage of *Z. variegata*. According to Richards ((49) p. 88) the strongly marked concentric lines on the thallus of this species are due to projecting flaps of tissue, but no other investigator refers to this.

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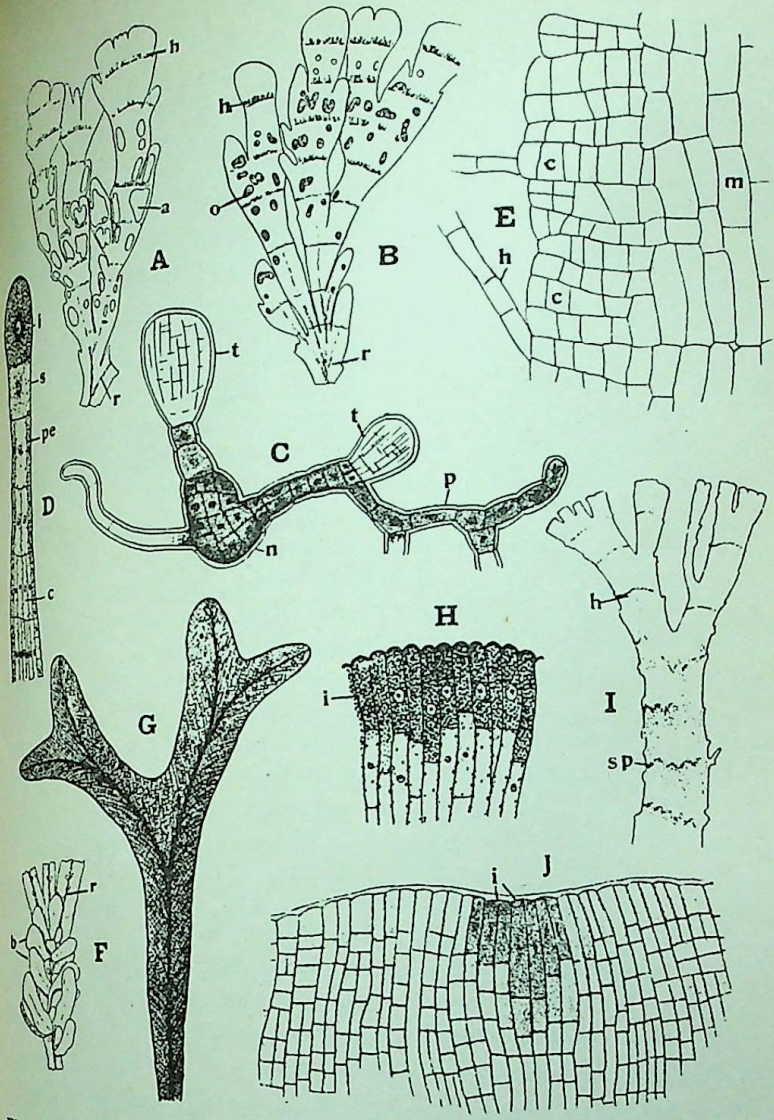

Fig. 110. A, B, D, F, H, *Zonaria Farlowii* Setch. & Gardn.; A, habit of male and B, of female plant; D, median longitudinal section through apex of thallus; F, lower part of an older frond, showing adventitious branching; H, edge of thallus in surface-view. C, E, J, *Dictyopteris membranacea* (Stackh.) Batt.; C, early stage in development; E, longitudinal section of midrib; J, apex of thallus in surface view. G, *D. delicatula* Lamour. I, *Taonia atomaria* (Woodw.) J. Ag., part of a thallus. *a*, antheridial sori; *b*, adventitious shoots; *c*, cortex; *h*, hairs or zones of hairs; *i*, initial cells; *m*, medulla; *n*, nodule; *o*, oogonial sori; *p*, protonemal threads; *pe*, surface cell; *r*, rhizoids; *s*, segment; *sp*, zones of sporangia; *t*, young frond. (C, E, I, J after Reinke; G after Boergesen; the rest after Haupt.)

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perennial on British shores, is widely distributed over the surface of the earth, but the chief centre of the genus is in warmer seas. The habit (fig. 110 G) is that of a small and rather delicate *Fucus*, a resemblance emphasised by the midrib traversing the thallus-segments; the stalk of older plants is formed by the persisting midrib. The base of the thallus is covered by a dense felt of rhizoids from which, as in the preceding genera, a number of plants usually arise. Tufts of hairs are scattered over the whole surface; Boergesen's figure ((9) p. 216) of *D. delicatula* indicates that they are formed in the same way as in *Padina*.

The apical initials ((40) p. 347, (46) p. 446, (47) p. 38) have the same shape as in *Padina* (fig. 110 J). Four or five of the median ones (*i*), which are longer and filled with denser cytoplasm than the rest, give rise to the midrib; they often occupy a slight depression. These particular initials exhibit abundant division, but the activity of those on either side gradually diminishes towards the margin, and Oltmanns ((44*a*) p. 180) is perhaps justified in regarding the median initials as the true meristem. The dichotomous branching commences with a multiplication of these cells, which is followed by the differentiation of two separate groups. Adventitious branches (cf. also (41) p. 156) may arise in four longitudinal rows from single surface-cells situated along the edges of the midrib. As in *Zonaria*, they develop rhizoids at their base and no doubt serve for vegetative propagation, which is also stated ((47) p. 43) to take place readily from pieces of the thallus.

The wings consist of two layers at the margins and of 4–6 layers near the midrib. The latter shows some differentiation ((37), (47) p. 37) into elongate medullary (fig. 110 E, *m*) and more or less isodiametric cortical cells (*c*). The midrib increases in thickness by tangential division of the surface-layer (fig. 110 E) and, as the wings wear away in the older parts, the exposed edges of the midrib become covered with a similar meristematic layer. In certain species (*D. delicatula* ((9) p. 216) a special group of small elongate cells, with oblique end-walls and thick cellulose membranes traversed by pit-canals, are found within the margins of the wings.

The remaining genera have not been so fully studied. In *Spatoglossum* ((3) p. 111, (4) p. 35) the broad thallus-segments are branched in a pinnate or subpalmate manner as a result of unequal development of the dichotomies; growth is by means of a marginal meristem. The monotypic *Lobospira* ((4) p. 96, (5) p. 363, (25) pl. 34) shows pronounced pinnate branching in a single plane. The older axes, as a result of growth in thickness, gradually become cylindrical, while the numerous short flattened, and not uncommonly incurved, laterals become orientated in diverse directions owing to twisting of the axes. For details of the other genera distinguished by Agardh, see (4) and (38) p. 186.

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THE ASEXUAL REPRODUCTIVE ORGANS

These, the so-called tetrasporangia, constitute one of the characteristic features of Dictyotales. They are nearly always found on distinct asexual individuals, although Holden (30) has recorded them both on male and female plants of *Dictyota* (cf. also (14) p. 55). The sporangia themselves display considerable uniformity, but their diverse arrangement in the different genera affords features of taxonomic importance (44,47,60). They are spherical (*Dictyota*, fig. 108 G, *sp*) or pear-shaped (*Padina*, fig. 111 F, *sp*; *Zonaria*, fig. 111 C, *sp*) superficial outgrowths, which are usually separated from the parent-cell by a transverse septum, although this is lacking in some species of *Zonaria* (fig. 111 C). The small basal cell sometimes (*Dictyopteris*) undergoes a second transverse division. It is usually embedded in the peripheral layer (fig. 108 G, *b*), although in *Dictyota* (29) it is stated to become elevated into the sporangium like a columella as a result of accumulation of mucilage between wall and protoplast and to project markedly above the surface after dehiscence; it is suggested that this protrusion of the basal cell may play an active part in spore-discharge. The sporangia generally project well above the surface, but in *Taonia* they are partially sunk.

During the enlargement of the sporangium ((13), (28) p. 248, (69)) the nucleus increases greatly in size, often becoming elliptical with the long axis parallel to the surface of the thallus and, when this is so, it twists through a right angle before division takes place. Centrosomes have usually been recorded. The first nuclear division, after the basal cell has been cut off, is meiotic (13,21,22,28,43,69), and is normally followed by only one further division. After this the cytoplasm undergoes cleavage about the four nuclei to form the naked tetraspores (cf. also (36)), which are usually arranged crosswise when viewed from above, although a tetrahedral grouping (fig. 108 G) is not uncommon. In some species of *Zonaria* (*Z. flava* (52) p. 68; *Z. Farlowii* (28) p. 248) there is a third division in the sporangium (fig. 111 B) resulting in the formation of eight spores, which in *Z. Farlowii* are separated by delicate septa (fig. 111 C). The mature spores generally round off before being set free through the gelatinised apex of the sporangium. Soon after liberation the large motionless spores secrete a cellulose membrane and can then develop directly into a new plant; in fact germination sometimes occurs within the sporangium ((28) p. 249, (47) p. 7).

In *Dictyota* the tetrasporangia occur singly or in small groups on both surfaces of the flat fronds (fig. 108 G, *sp*) and show no relation to the tufts of hairs. In most of the other genera, however, their distribution is connected with that of the hairs. Thus, in *Dictyopteris* the sporangia are grouped around the tufts. In *Padina pavonia* ((47) p. 22) they develop in several rows on either side of the zones of hairs (fig.

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111 F) situated on the lower (sometimes also on the upper (7) p. 259) surface of the fan. Since the hairs usually die during the development of the sori, the latter form characteristic double, brown-coloured, bands upon the surface (fig. 109 B, *sp*). In weak plants the sorus develops only along the anterior margin of each series of hairs ((11) p. 87), and this is the normal condition in *P. Sanctae Crucis* ((9) p. 201), where, moreover, a sorus is associated only with every second band.

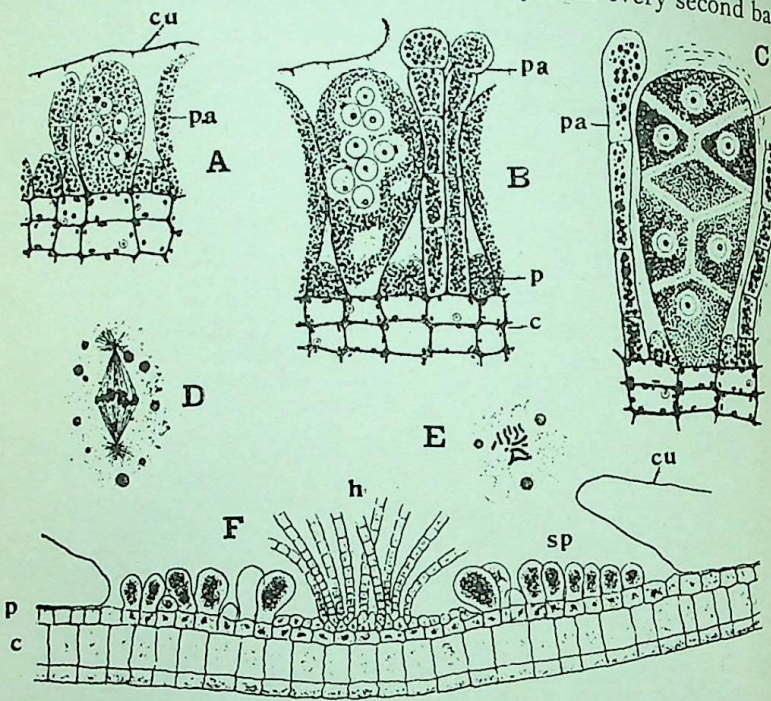

Fig. 111. A–E, *Zonaria Farlowii* Setch. & Gardn.; A–C, successive stages in development of a sporangium, C practically mature; D, metaphase of heterotype division; E, polar view of metaphase of third nuclear division in the sporangium. F, *Padina pavonia* (L.) Gaill., section through a sporangial sorus. *c*, central cells; *cu*, cuticle; *h*, hairs; *pa*, paraphysis; *sp*, sporangium. (F after Oltmanns; the rest after Haupt.)

Another variation is seen in *P. gymnospora*, where the sori are situated between the bands of hairs.

The sori of *Taonia* ((47) p. 30, (62) p. 460, (63) p. 362) exhibit essentially the same arrangement (fig. 110 I, *sp*). Both here and in *Padina* scattered sporangia are also found, and this compares with the condition in *Zonaria* where the sori form clearly circumscribed areas between the bands of hairs when these are present (28, 52); in *Z. variegata* they occur on the upper surface of the prostrate thallus. The sori of *Zonaria* often show a centrifugal development and are distinguished by the presence among the sporangia of colourless multicellular paraphyses of characteristic form (fig. 111 B, C, *pa*) which give the

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sori a speckled or even whitish appearance. In the little-known genus *Glossophora* ((3) p. 108) all the reproductive organs are borne on small ligulate outgrowths which arise in large numbers from the upper parts of the forked band-shaped thalli.

The developing sporangia of a sorus gradually elevate the "cuticle" (fig. 111 A, *cu*) which, although it may persist for some time as a protective covering, is ultimately burst (fig. 111 B, F, *cu*). In *Zonaria variegata* ((52) p. 76) the marked gelatinous thickenings of the outer walls of the sterile cells intermingled with the sporangia aid in raising the cuticle, a rôle perhaps fulfilled by the paraphyses of other *Zonarias*.

In *Taonia* the germlings develop into mature thalli in about 30 days and during this period there are formed some 60 zones of tetrasporangia so that a definite correlation between the daily tidal rhythm and the initiation of the zones is suggested ((50) p. 115). A similar periodicity in soral development is likewise probable in *Padina* and other instances ((18) p. 245), where the sori arise successively from a marginal meristem. In *Dictyota*, on the other hand, there is no evidence of any such relation; Williams ((71) p. 556) in fact states that sporangia of all ages are to be found throughout the season on the thalli of all British Dictyotales. Discharge of the spores in *Dictyota* and *Dictyopteris* is strongly favoured by light ((45) p. 332).

THE SEXUAL REPRODUCTIVE ORGANS

The oogonia and antheridia are usually borne on distinct individuals, although a few species (e.g. *Padina pavonia*) are monoecious (cf. also (39) p. 178). The sex organs are for the most part arranged in definite projecting sori, although the oogonia of *Spatoglossum* and of *Dictyopteris membranacea* are scattered singly or in small groups ((47) p. 42). In *Dictyota dichotoma* ((47), (60) p. 53, (70)) both kinds of sori are distributed over the greater part of the thallus, appearing elliptical when viewed from above and fan-shaped in sections (fig. 112 A, B). The outgrowing surface-cells remain in close apposition and gradually lift the "cuticle" (*cu*) which envelops the sorus until maturity; a small basal cell is cut off at an early stage. Each oogonium produces a single ovum which is liberated through the gelatinised apex, dehiscence usually advancing centrifugally; there are 25–50 oogonia in a sorus. Occasionally there are functionless oogonia at the margin ((70) p. 185).

The deep-brown colour of the female sori contrasts with that of the male ((59) p. 9, (70) p. 187) which appear as white glistening spots upon the thalli. The future male sori ((47) p. 10) become recognisable at an early stage by the disintegration of the chromatophores in an elliptical group of surface cells which grow out to form the antheridia. The cells at the margin of the group elongate like the others, but in them the chromatophores persist and retain their pigment. These cells (fig. 112 B, *st*) remain undivided and constitute three or more rows of involucral cells at the edge of the sorus; they are usually

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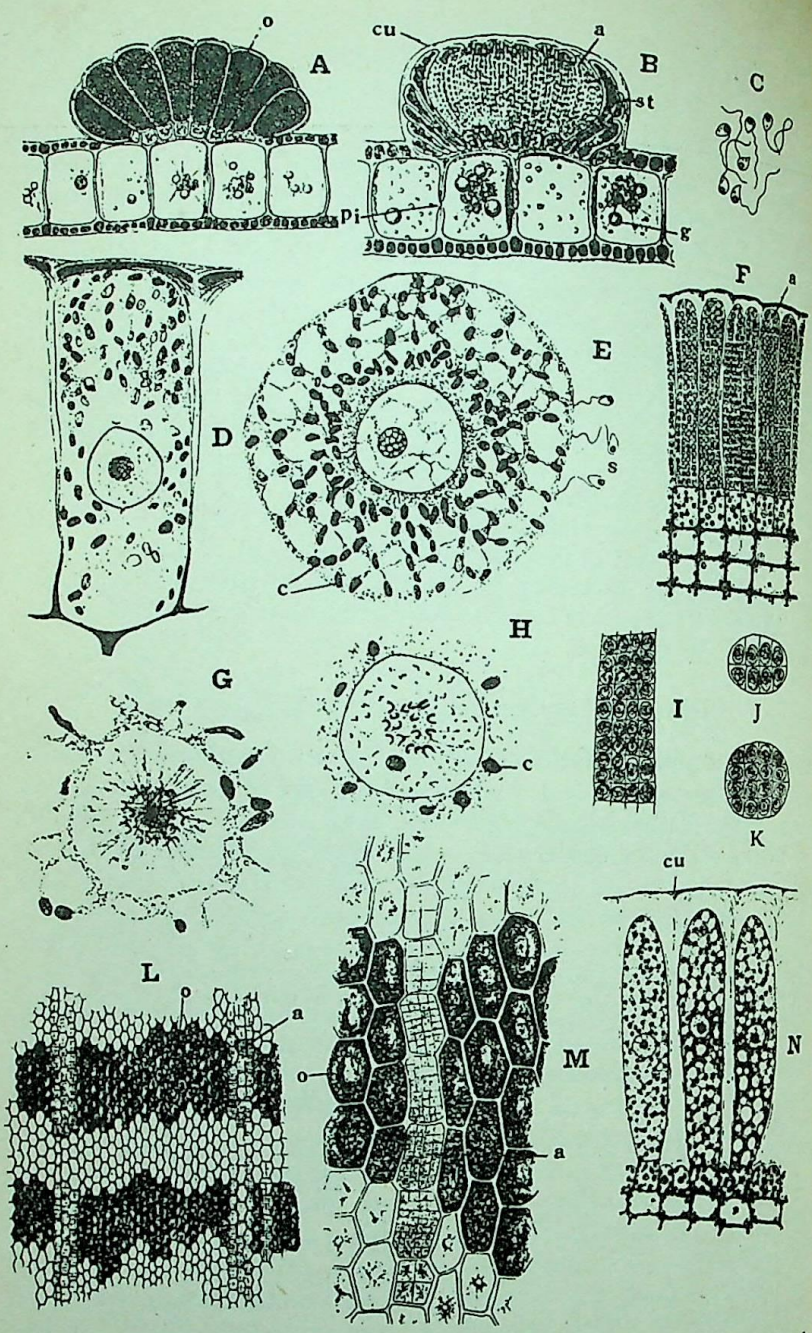

Fig. 112. A–E, G, H, *Dictyota dichotoma* (Huds.) Lamour.; A, oogonial and B, antheridial sorus in vertical section; C, spermatozoids; D, rudiment of oogonium before cutting off of the stalk-cell; E, fertilisation; G, polar view of nucleus during first division in zygote, 32 chromosomes; H, ditto during

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interpreted as sterile antheridia. The actual male organs (*a*) first segment by a vertical wall, perpendicular to the long axis of the thallus ((70) p. 189); this is followed by further vertical walls in other planes, and during this there is also extensive horizontal septation. In the mature, altogether colourless, antheridium 32–64 compartments separated by delicate septa are visible in the transverse and 20–24 tiers in the longitudinal section. There are 100–200 antheridia in a sorus and each forms about 1500 sperms.

Like the sporangia, the sex organs of *Padina pavonia* ((22), (47) p. 24) are produced in relation to the hairs which are shed during their development. The oogonia (fig. 112 L, *o*) form double concentric zones on either side of the bands of hairs on the lower surface. The basal cell usually divides transversely and the upper half may give rise to a second oogonium after the first has dehisced ((47) p. 25). The zones of oogonia are interrupted at variable intervals by radial rows of antheridia (fig. 112 L, M, *a*), the differentiation of which commences in the middle of each row and advances centrifugally towards apex and base of the thallus. The mature antheridia show about 32 chambers in transverse section.

The imperfectly known oogonial sori of *Taonia* ((47) p. 33) form short double transverse rows which are scattered over the thallus, while the milk-white male sori (51, 62) are situated on either side of and between the zones of hairs. In section they resemble those of *Dictyota*, although the antheridia do not all ripen simultaneously; the sori usually exhibit sterile marginal cells with yellowish chromatophores.

In *Zonaria* the sex organs are independent of the hairs and the sori lack the paraphyses found in the asexual ones. In *Z. flava* ((52) p. 68) they form continuous or interrupted zigzags, while those of *Z. Farlowii* (28) constitute irregular areas between the bands of hairs (fig. 110 A, B), the white male sori (*a*) in both species being larger than the female (*o*). In the latter only some of the cells grow out into oogonia (fig. 112 N), while in the male sori all the surface-cells produce antheridia and involucral cells are usually absent, although occasionally found in *Z. flava* and *Z. lobata* ((52) pp. 69, 72). In the mature antheridium of *Z. Farlowii* there are 20–40 tiers of cells, with 8 or 16 cells in each tier (fig. 112 I–K).

The scattered male sori of *Dictyopteris* ((37) p. 466) are of very diverse size, containing between 3 and 100 antheridia.

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division of oogonial mother-cell, 16 chromosomes. F, I–K, N, *Zonaria Farlowii* Setch. & Gardn.; F, section of part of male sorus; I, part of a longitudinal section of an antheridium; J, K, transverse sections of same; N, section of part of a female sorus. L, M, *Padina pavonia* (L.) Gaill., surface view of thallus showing transverse oogonial and longitudinal antheridial sori, on a larger scale in M. *a*, antheridium; *c*, chromatophore; *cu*, cuticle; *g*, refractive globule; *o*, oogonium; *pi*, pit; *s*, spermatozoid; *st*, sterile antheridium. (A, B after Thuret; C–E, G, H after Lloyd Williams; L, M after Reinke; the rest after Haupt.)

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The discharge of eggs and sperms takes place rapidly at about the time of daybreak. Both the septa and the walls of the ripe antheridia are dissolved ((28) p. 246, (51), (52) p. 69) so that the numerous minute male cells lie in a mass of mucilage occupying the space bounded by the involucral cells, when these are present. At this stage the male cells, formed singly from each compartment, appear rounded. Lloyd Williams (65, 66) first showed that they possess flagella, although Thuret ((59) p. 11) seems to have recognised something of the kind. According to the former, swarming of the sperms in *Dictyota* and *Taonia* depends on exposure to a sufficiently bright light and on the realisation of a certain temperature. The pear-shaped spermatozoids ((70) p. 190) have a large posterior nucleus and an eye-spot situated at the anterior end, while the single long, forwardly directed, flagellum arises near the eye-spot (fig. 112 C); there is reason to suspect the presence of a second, very short, backwardly directed flagellum, although this has not so far been demonstrated. Williams, who observed fertilisation ((70) p. 191), states that freshly discharged ova exert a great attraction on the sperms (fig. 112 E), although, if the eggs are not fertilised within $\frac{1}{2}$ to $\frac{3}{4}$ of an hour, they become invested by a membrane and germinate parthenogenetically. The male nucleolus can be recognised within the fusion-nucleus after fertilisation; the single centrosome later divides into two.

In British waters *Dictyota dichotoma* shows a regular fortnightly production of sexual sori from July onwards, corresponding to the interval between two spring tides (67, 71). The sori are initiated during a period of neap tides, and liberation of the sexual cells takes place at a variable number of tides after the highest spring tide (3–5 in the Menai Straits; 7–12 at Plymouth). At this time the rudiments of the next crop of sori begin to appear. A similar rhythm is observed in plants kept in the laboratory, and according to Hoyt (34) it is also shown by the new thallus-branches that arise in cultures and have never been exposed to the influence of the tides. The same rhythm is, moreover, maintained when the light-conditions are experimentally reversed or when the tides are modified by wind. Williams ((71) p. 548) concludes that the periodicity in question is hereditary, but that on British shores the time of development of the sexual sori is regulated by the greater illumination available during the low water of spring tides. There is some evidence that a similar periodical production of oogonia takes place in *Dictyopteris* ((71) p. 553), but other Dictyotales do not appear to exhibit this rhythm. Comparison should be made with similar features in *Nemoderma* (p. 124) and Fucales (p. 377).

The behaviour of *Dictyota* has also been investigated in other localities (32, 34, 42). A similar, though less marked, fortnightly production of sexual sori takes place at Naples, where *D. dichotoma* occurs at some depth and the tidal differences are slight; here, as in the laboratory cultures, illumination can scarcely be a factor. On the other hand, in Jamaica, where the tides are irregular, periodicity is scarcely evident.

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On the shores of North Carolina the successive crops of sexual sori are produced at monthly intervals (spring tides of full moon).

THE EARLY DEVELOPMENT OF THE THALLUS

The germination of the tetraspores shows certain differences in the individual genera. The first wall is stated to be perpendicular to the direction of the incident light in *Dictyota* and *Dictyopteris* ((36) p. 215, (45) p. 340), although Reinke concluded, from the observation of spores germinating within the sporangia of *Dictyota*, that it is the end of the spore directed away from the parent-thallus that becomes the apex of the new plant. In *Dictyota* ((15), (47) p. 8) the upper segment becomes the apical cell of the embryo, while the lower produces a rhizoid. Reinke records diverse abnormalities. The segments of the apical cell divide into an inner and four outer cells, the latter dividing anticlinally to form the surface-layer of the cylindrical embryo. Later colourless multicellular rhizoids grow out from the superficial cells. The summit of the embryo soon broadens to form the band-shaped thallus, while its basal portion gives rise to more or less numerous lateral branches, some of which become prostrate and form the rhizome.

In most Dictyotales, however, the germinating spores first produce a multicellular oval body ((13) p. 154, (47) p. 23), well seen in *Padina* (fig. 109 E, G–I, *n*). One of the superficial cells of this *nodule* becomes protruded to form the apical cell of a cylindrical shoot (fig. 109 I, *e*) which later flattens at its apex and slowly passes over into the adult fan. Other cells of the nodule subsequently grow out in the same manner (fig. 109 E), although some of the resulting shoots usually remain arrested; other surface-cells give rise to rhizoids (*r*). In *Taonia* ((47) p. 31, (50) p. 118) one of the cells formed by the first transverse division of the spore grows out into a rhizoid and the formation of the nodule takes place subsequently. One of its superficial cells, determined ((50) p. 118) by the direction of the incident light, enlarges to form an apical cell which, however, only cuts off a few segments before dividing longitudinally to form a number of initials.

Much the same occurs in *Dictyopteris* ((47) p. 41, (48) p. 125), although here the cells of the nodule (fig. 110 C, *n*) sometimes grow out into branched uniseriate threads (*p*) attached to the substratum by rhizoids and growing by means of an apical cell; from this protonema a number of fronds (*t*) arise as lateral outgrowths. More usually, however, the outgrowing cell of the nodule develops direct into a mature plant. The young fronds may remain one-layered for a long time (cf. also (17) p. 444).

Reinke ((47) p. 9; cf. also (69) p. 155) records the development of embryos from entire sporangia in *Dictyota* and compares this with the formation of adventitious branches. In *Padina* he describes ((47) p. 24)

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the occasional liberation and germination of the entire sporangial contents in individuals that do not produce any tetraspores. Robinson ((50) p. 117) observed similar phenomena in *Taonia*, although here such abnormal stages are encountered side by side with tetraspores. In *Padina* they show no differences in germination, but in *Taonia* they exhibit greater powers of resistance and a greater capacity for germination than the tetraspores, while the resulting plants are larger and display more vigorous growth.

The germination of zygotes and tetraspores appears to take place in the same way, although that of the former has not often been studied.

THE LIFE-CYCLE

The full life-cycle has only been investigated in *Dictyota dichotoma* (68-70), *Padina pavonia* (13,21,22), and *Zonaria Farlowii* (28). The isomorphic alternation, indicated by the distribution of the reproductive organs, is fully confirmed by the cytological data and has also been demonstrated experimentally in *Dictyota* and *Padina variegata*. Hoyt (33) and Wolfe (72) used the faculty of tetraspores and zygotes to germinate on oyster-shells placed in cultures of asexual and sexual plants respectively, the shells bearing the germlings being subsequently submerged in their natural habitats; all adjacent plants of the species experimented with were removed. It was thus established that, as a general rule, tetraspores give rise to sexual and zygotes to asexual plants (cf. also (54) p. 270). Data were also obtained that indicated a production of equal numbers of male and female plants, suggesting segregation of the two sexes at the reduction divisions. Schreiber ((54) p. 272), using methods similar to those employed for *Laminaria* (p. 248), definitely proved that in *Dictyota* two of the four spores of a sporangium develop into male and two into female plants. It can scarcely be doubted that this will be found to apply to Dictyotales generally and that all members of the order possess an isomorphic alternation with genotypic sex determination. Although the two generations often occur simultaneously, there is evidence of some seasonal succession ((47) p. 13, (54) p. 266).

Parthenogenesis does not appear to play an important rôle among Dictyotales (cf. (39) p. 185), although germination of unfertilised ova is not uncommon ((47) pp. 11, 26, (72) p. 86). Lloyd Williams ((67), (70) p. 196, (71) p. 553) found that such ova exhibit irregularities in nuclear division and that segmentation soon ceases; this is followed by the death of the germlings.

Many investigators comment on the great preponderance of asexual over sexual plants and in some regions only tetrasporangiate individuals have been found.[1] No adequate explanation of these facts is at present forthcoming, but the repeatedly recorded germination of

[1] See (13) p. 139, (20) p. 364, (28) p. 244, (47) p. 33, (50) p. 114, (52) p. 68, (53) p. 62, (69) p. 156.

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the entire contents of a sporangium (p. 317)—presumably without the occurrence of reduction—and the occasional greater vigour of such germlings as compared with those formed by tetraspores, may indicate a method of multiplication of the diploid phase without the intervention of a sexual one ((39) pp. 182, 184, (69) p. 156). Abundant vegetative propagation may, moreover, help in the rapid multiplication of the asexual generation.

On the other hand, although Carter (13) only met with tetrasporic plants of *Padina pavonia* in British waters, he nevertheless found that they formed tetraspores in the normal manner with accompanying reduction. This shows that the foregoing explanations will not account for all the facts. Since it is hardly likely that all the haploid spores perish, one is forced to assume either that there is a microscopic sexual generation or perhaps more probably that the latter inhabits deep water. In this connection it may be noted that, according to Lloyd Williams (67), the spores and zygotes of *Dictyota* germinate in the summer, but the germlings remain small until the following June.

THE AFFINITIES OF THE DICTYOTALES

Owing largely to the possession of tetraspores and of male cells, which were long thought to be motionless, the Dictyotales have often been regarded as related to the Red Algae ((18) p. 169) and have indeed occasionally been directly referred to that class. As a matter of historical interest it may be mentioned that both Thuret and Cohn regarded the oogonial sori as equivalent to the cystocarps of the Rhodophyceae. There is, however, no sound basis for envisaging any affinity with Red Algae. The pigmentation of the chromatophores, the metabolic products, the type of swarmer as exemplified by the spermatozoid, and the plurilocular nature of the antheridia all indicate a close affinity with other Phaeophyceae. Even the tetrasporangia no doubt merely represent a specialisation of the unilocular sporangium, and in this connection the frequent formation of eight spores in *Zonaria* is significant. It should, moreover, be recalled that in diverse Ectocarpales (p. 118) and Tilopteridales (p. 153) the unilocular sporangia produce only few spores, which are then occasionally developed as aplanospores or liberated as motionless cells.

The exact relation of the Dictyotales to other Brown Algae is obscure and they appear as a specialised line that originated from simple isomorphic forms and has departed rather widely from the normal type. Sauvageau ((52) p. 80) supports an affinity with Cutleriales, a view which is largely based on the close resemblance in habit and structure between *Zonaria variegata* (p. 308) and the *Aglaozonia*-stages. Particular stress is laid on *Aglaozonia canariensis* ((8), (11) p. 77, (31) p. 591, (52) p. 79), for which at present no corresponding *Cutleria*-stage is known. Here the pyriform sporangia in the small and scat-

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tered sori are not in lateral contact and are not cut off from the cell which produces them so that there is considerable resemblance with the sori of *Zonaria variegata*.

THE GENUS *DICTYOTOPSIS* (61)

It is difficult to assign a position to this remarkable genus which in various respects recalls one of the simpler Jungermanniales (*Metzgeria*). The cells, however, possess brown-coloured chromatophores devoid of starch and include probable fucosan-vesicles. The thallus (fig. 113 A) is one-layered and devoid of a midrib; it shows dichotomous branching, with one fork usually growing more strongly than the other, while the recurved margins bear multicellular, little-branched rhizoids (*r*). The

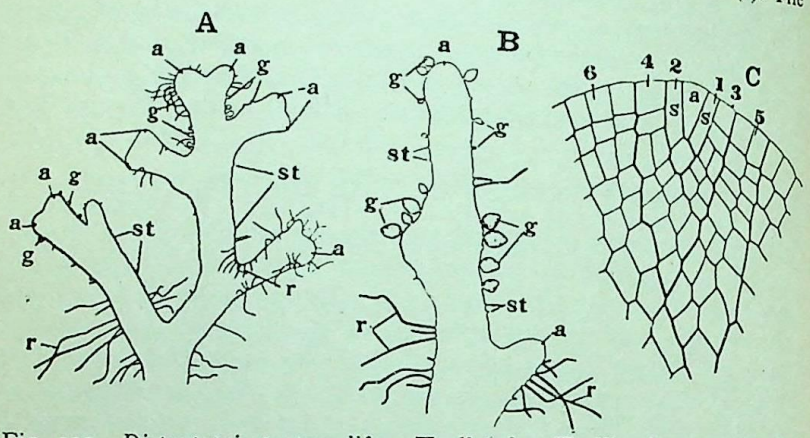

Fig. 113. *Dictyotopsis propagulifera* Troll (after Troll). A, part of thallus from below, the margin occupied by rhizoids (*r*) and the stalks (*st*) of propagules; B, the same enlarged, with mature propagules (*g*); C, apex enlarged showing segmentation, 1–6 successive segments. *a*, apical cells; *g*, propagules; *r*, rhizoids; *s*, segment; *st*, stalks of shed propagules.

large apical cell (fig. 113 C, *a*) is two-sided. The only method of reproduction so far observed is by ovoid, one-layered propagules borne on two-celled stalks along the margins of the thalli (fig. 113 B, *g*). After cutting off a certain number of segments the apical cell of the propagule remains dormant until detachment has occurred; the propagules are thus arrested laterals.

The alga is a member of the Eastern Mangrove-community and in part inhabits mud that is inundated only at the time of spring tides; at lower levels it constitutes a thick covering on the projecting respiratory roots of *Sonneratia*.

The type of apical cell and its mode of segmentation (fig. 113 C) are unique among Brown Algae. The abundant formation of propagules recalls *Sphacelaria*, with which, however, there is practically no other resemblance, and, until other types of reproductive organs become known, the systematic position must remain quite doubtful.

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Order IX. *FUCALES*

The numerous seaweeds belonging to this order are, like the Laminariales, diploid and characterised by marked morphological differentiation and anatomical complexity, but in many respects the two orders diverge widely from one another. No member of Fucales attains the huge dimensions reached by some Laminariales. The broad discoid holdfasts (figs. 114, 120) are very distinctive, while all the typical Fucales exhibit apical growth by means of an apical cell (figs. 126, 127) of characteristic shape (p. 349). Apart from the copious sexual reproduction, multiplication is effected solely by vegetative means. The sex organs are located within the conceptacles (fig. 133) which constitute one of the chief characteristics of the order. Reduction occurs during gametogenesis, and no distinct haploid generation is organised so that there is no alternation. The peripheral

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cells harbour numerous oval chromatophores, and centrosomes (fig. 3 *D, c*) are usually recognisable during nuclear division.

Despite great diversity in outward habit, the germlings developed from the zygotes show considerable uniformity and this, no less than other distinctive features (apical growth, conceptacles) speaks for a monophyletic origin. There are, however, a number of aberrant forms (Hormosiraceae, Durvilleaceae) whose exact relation to the main series is not at present clear.

In the Northern Hemisphere the Fucales are largely surf-loving forms, many of them inhabiting the littoral region where they often display a marked zonation in relation to a varying capacity for drought-resistance (p. 382). Several genera (*Halidrys*, *Cystoseira*), however, occur in the sublittoral region or in permanent pools near low water mark, where they are only exposed occasionally during spring tides. The warm-water forms (*Turbinaria*, *Sargassum*) practically always grow permanently submerged, while the bulk of the New Zealand Fucales grow at and below low tide level ((176) p. 497, (306)).

The Fucales attain their greatest development in the colder seas. Species of *Fucus* are abundant in North Temperate waters (see map 2, p. 252) and with them are associated *Pelvetia*, *Ascophyllum*, *Himanthalia* and *Halidrys*. The large genus *Cystoseira* is also largely confined to the Northern Hemisphere, though more abundantly represented in the warmer seas (Mediterranean, Indian and Pacific Oceans); some species are known from South Africa. The Fucales also show an extensive development in the Southern Hemisphere, and diverse distinctive genera are recorded from Australia and New Zealand (*Carpoglossum*, *Phyllospora*, *Scaberia*, *Cystophora*, *Marginariella*, *Seirococcus*, *Landsburgia*, *Myriodesma*, *Xiphophora*, *Notheia*, *Hormosira*); the last three are endemic ((131) p. 307), whilst *Landsburgia* and *Marginariella* are confined to New Zealand. The wealth of Fucales in the Australasian region is in striking contrast to their paucity in South Africa. The Australasian region seems also to be one of the chief centres for *Sargassum*, although the latter has representatives in all warmer seas and is widely distributed in tropical waters (see map 2, p. 252). *Turbinaria* seems to have its main centre in the Eastern Tropics, though a few species extend south to the Cape and Australia and northwards to China ((15) p. 217). The remarkable *Durvillea* is subantarctic in distribution (New Zealand, Falkland Isles, Cape Horn, Kerguelen). *Coccophora* (*C*, see map 2, p. 252) is so far only known from Japan ((174) p. 591), where too most species of *Cystophyllum* are found.

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EXTERNAL MORPHOLOGY

(*a*) *Fucus* and its Allies (Fucaceae)

The many species of *Fucus* are essentially characteristic of North Temperate and Arctic regions. The repeatedly forked band-shaped thalli (fig. 114 A), narrowed below into a short stalk (*s*) terminating in the discoid attaching organ (*d*), are familiar to every student of Botany. The branching is dichotomous and in one plane, although one or other limb is commonly favoured. The flattened segments are traversed by a prominent midrib (*r*) which thickens in the older parts where it passes over into the stalk (*s*); the latter is, in fact, largely composed of the midrib of the first-formed part of the thallus, the wings of which have been worn away by wave-action. The tip of every growing branch is occupied by a narrow groove extended in the plane of flattening and filled with mucilage; at the base of this the apical cell is situated. The wings usually bear irregularly scattered sterile conceptacles or *cryptoblasts* (fig. 114 A, *c*), while at certain times of the year the tips of the branches are more or less markedly swollen (*f*) and harbour the large fertile conceptacles, within which the sexual organs are produced. In these fertile tracts or *receptacles* the midrib is lacking; their inflation is due to abundant production of mucilage ((215) p. 190).

The young plants (cf. also p. 347), which to begin with are nearly spherical (fig. 114 G) as in all Fucales, soon become cylindrical and then club-shaped as a result of broadening at the top (fig. 114 B); at this stage an apical depression appears, from which a number of hairs (*h*) arise. By degrees most of the embryo flattens, although the basal part remains cylindrical and constitutes the beginnings of the stalk. As forking sets in, the mature thallus-form is assumed. Adventitious laterals occasionally develop (fig. 114 B, *a*) from the stalk of the young plant ((178) p. 5). In *F. dichotomus* Sauv. ((228) p. 25), in which the fronds last for one year only, these laterals regenerate the plant in the next season.

The British species are in general readily distinguished and comprise: *F. serratus* ((80) pl. 47; fig. 114 C), with a serrate margin and flattened receptacles (*f*); *F. vesiculosus* ((80) pl. 204; fig. 114 D), with a smooth margin, conspicuous and commonly paired air-bladders (*v*; absent in var. *evesiculosus*), and swollen receptacles (*f*); *F. spiralis* (*F. platycarpus* Thur., fig. 114 A), smaller than either of the preceding, devoid of air-bladders, and with dilated irregularly swollen fertile tips (*f*) which have a sterile border (*b*); and *F. ceranoides* L. ((80) pl. 271), especially common in brackish water, with a delicate thallus, showing regular dichotomy and bearing slender fusiform receptacles. Soft irregular swellings, due to internal accumulation of gases, are not uncommon in the first three species, especially in brackish water ((14) p. 328, (228) p. 86). *F. spiralis* is hermaphrodite (similarly *F. dichotomus* (226)); *F. vesiculosus* and *F.*

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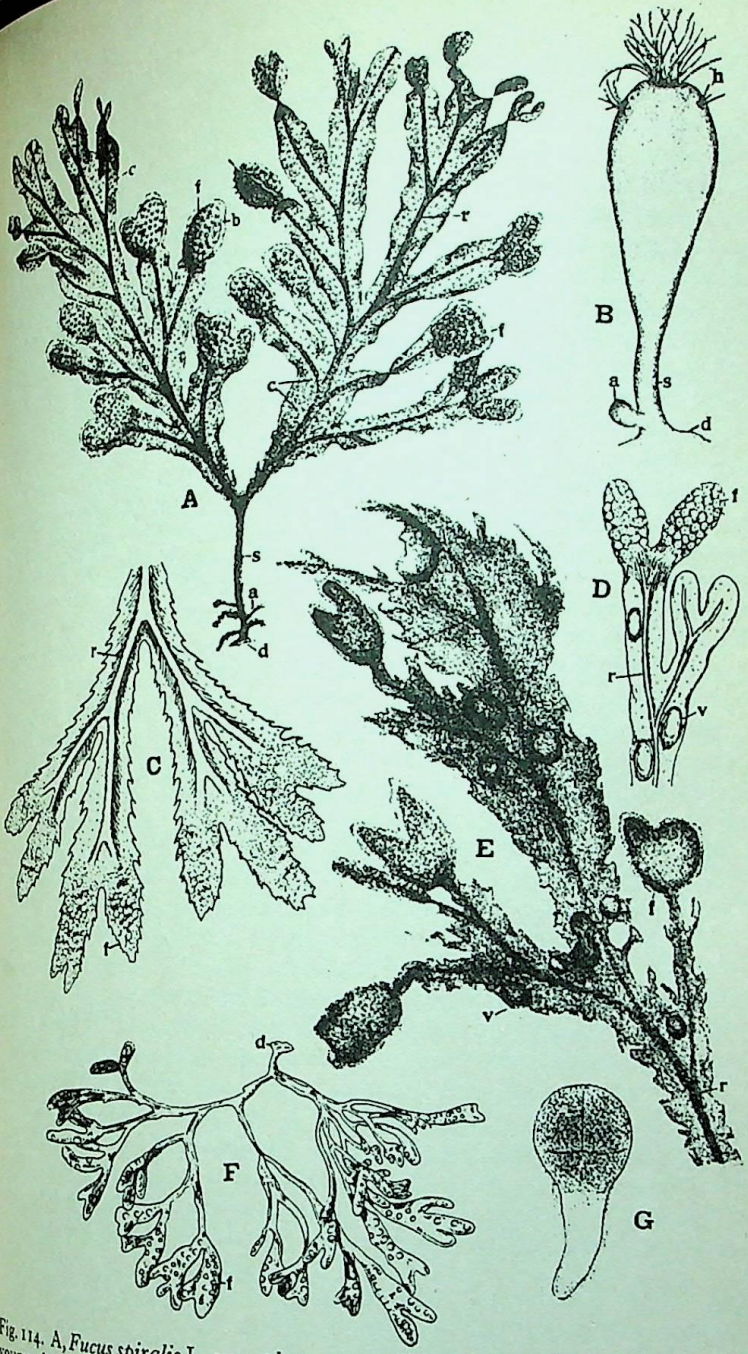

Fig. 114. A, *Fucus spiralis* L. var. *platycarpus* (Thur.) Batt. B, *F. vesiculosus* L., young plant. C, G, *F. serratus* L.; C, part of thallus; G, embryo. D, *F. vesiculosus* L., apex of thallus. E, supposed hybrid between *F. spiralis* and *F. vesiculosus*. F, *Pelvetia canaliculata* (L.) Decsne & Thur. *a*, adventitious fronds; *b*, border of receptacle; *c*, cryptoblasts; *d*, attaching disc; *f*, receptacle; *h*, hairs; *r*, midrib; *s*, stalk; *v*, air-bladder. (A, E after Sauvageau; B after Oltmanns; G after Thuret & Bornet; the rest after Fritsch & Salisbury.)

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serratus are dioecious, whilst *F. ceranoides*, though mostly dioecious (31, 63), is occasionally hermaphrodite ((160) p. 437, (254)). *F. spiralis* and *F. ceranoides* are generally found near high-tide limit, whilst the other two species extend over a large part of the littoral region, *F. serratus* inhabiting more especially the lower levels. *F. vesiculosus* favours localities where there is a strong swirl ((165) p. 297, (166) p. 173, (253) p. 45). At the limits of the zones occupied by the diverse species a number of transitional forms are often found, but there is no support for Stomps' view (254) that *F. vesiculosus*, *F. spiralis*, and *F. serratus* are but varieties of a single species (cf. (156) p. 145, (228) p. 76). Observations of Nienburg ((168) p. 8) and Rees (193) indicate that the North European species of *Fucus* do not in general live for more than 3 or 4 years and that only in more sheltered habitats (cf. also (215) p. 94); growth is rather slow ((78), (133), (138)).

The designation of the species above described as *F. spiralis* has been the subject of much debate (see (21) p. 472, (23), (90) p. 581, (215) p. 70). Sauvageau ((215) p. 73), who maintains the name *platycarpus* on the grounds that the *F. spiralis* of Linnaeus is insufficiently defined, concentrated attention on the two forms of this species. That described by Thuret as *F. platycarpus*, which bears its receptacles in lateral series and in which the sterile border is well marked (fig. 114 A), is rather rare in Northern Europe and extends farther southwards ((40), (234) p. 30) than the other; according to Rees ((194) p. 85) it inhabits more sheltered situations. Sauvageau's var. *spiralis* (incl. *F. Areschougii* Kjellm. (21) p. 475, (216) p. 295) is in general smaller and shows a corymbose grouping of the receptacles, which are often subglobose and have an ill-defined border; twisting or spirality of the fronds is not invariable. This occurs in exposed habitats. In this country, where it is regarded as the type, Thuret's form is known as var. *platycarpus* (Thur.) Batt.

Other widespread species of *Fucus* are: *F. evanescens* C. Ag. ((66) p. 11, (157) p. 66, (299) p. 14) and *F. inflatus* L. ((21) p. 465, (60), (190) p. 209), both abundant in the North Temperate zone up to the Arctic, the former with broad leathery fronds in which the midrib fades in the ultimate segments; the North American *F. edentatus* De la Pyl. ((66) p. 28), with regular dichotomous branching, no air-bladders, and elongate receptacles; and *F. axillaris* J. Ag. ((228) p. 96), possibly only a form of *F. vesiculosus* (147), found on the coasts of Spain and Portugal and distinguished by the frequent presence of bladders at the points of forking of the fronds. The only Mediterranean species is the small *F. virsoides* J. Ag., which is confined to the littoral region of the Adriatic ((55), (232), (273) p. 11, (315) p. 184); Sauvageau ((215) p. 146, (228) p. 24) regards it as a form of *F. spiralis*, probably introduced by shipping.

Hesperophycus (65) has the same habit as *Fucus*.

Compared with *Fucus*, *Pelvetia* appears as a specialised form suited to an extreme environment. *P. canaliculata* ((178), (275) p. 41) is widely distributed in the North Atlantic, where it forms a characteristic girdle at the uppermost limit reached by spray. The thallus shows adaptations to the prolonged exposure to desiccation during intertidal

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periods. It never reaches any considerable dimensions and dwarfing is the more marked, the higher the plants grow, the uppermost ones rarely exceeding 3–5 cm. in height. The narrow segments of the repeatedly forked thallus (fig. 114 F) are channelled, as implied by the specific name; during low water moisture is retained for some time within the channel, whilst the somewhat edgewise position of the wings reduces the degree of exposure to the midday sun. There is no midrib. The depression harbouring the apical cell is readily seen. There are no cryptoblasts, whilst the irregularly swollen receptacles (fig. 114 F, *f*) render fertile plants very conspicuous. The thallus is stated invariably to be occupied by an ascomycetous fungus (*Mycosphaerella Pelvetiae* (257)).

P. fastigiata (J. Ag.) De Toni (155), abundant in somewhat less extreme habitats on North Pacific coasts, though larger, has essentially the same habit. The receptacles are not so sharply defined and there are occasional cryptoblasts. Another similar form found in the same region is *Pelvetiopsis* ((65) p. 320).

A different habit is seen in *Ascophyllum nodosum* ((142), (178) p. 29, (197) p. 352, (275) p. 42), abundant on somewhat protected shores where it occurs together with *Fucus vesiculosus* in the upper part of the littoral region (fig. 117 B). The mature thallus (fig. 115 F) consists of dichotomously branched strap-shaped axes (*a*) bearing numerous short laterals (*la*), which often arise in tufts from narrow marginal slits and are commonly subopposite in arrangement (fig. 115 D). *Ascophyllum* thus combines dichotomous and monopodial branching. The fronds may be 1½ metres long; they are devoid of a midrib and are usually dilated at intervals by conspicuous vesicles (*b*) so that at high water the thallus spreads out near the surface. In adult plants the tips of the upper laterals become swollen and constitute receptacles (fig. 115 E, F, *r*). According to Tobler ((276) p. 575) the greater part of the long shoots perishes at the end of each season, but this is probably not so in all areas (cf. (141)).

The young plants ((178) p. 30, (275) Pl. XX) soon become elongate and show but little broadening above the basal stalk; the apex is truncate and devoid of hairs (fig. 127 C). In somewhat older germlings a number of laterals (*bs*) arise near the base, but these at first remain short, whilst the main axis grows rapidly and soon forms marginal branches of limited growth (fig. 115 C, *la*); at a later stage the basal laterals (*bs*) also lengthen, those originating close to the base subsequently appearing to arise directly from the attaching disc. If the axis is broken or damaged near its base, one of the basal shoots takes its place, whereas injury to the upper part of an older plant leads to the outgrowth of a number of the laterals into long shoots and results in a bushy habit. There is altogether much diversity in the appearance of this seaweed.

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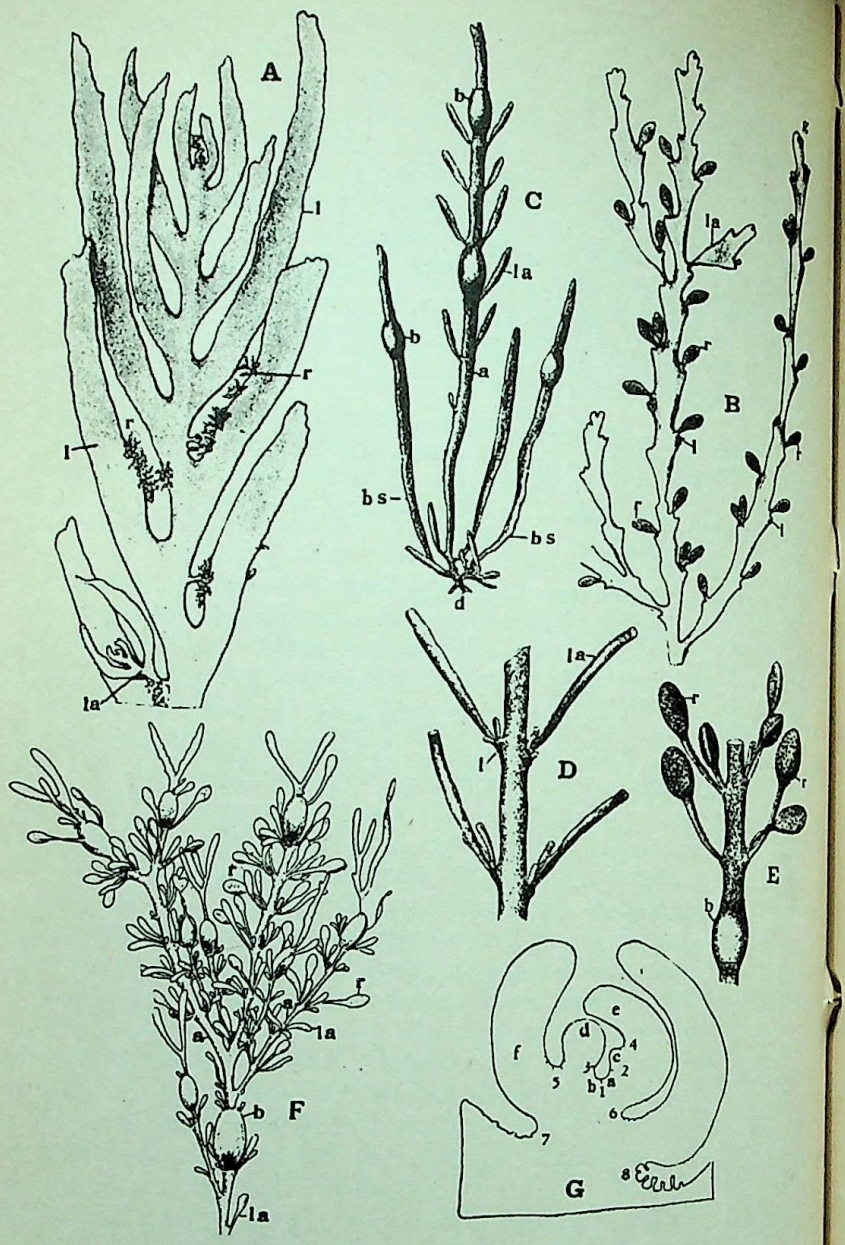

Fig. 115. A, G, *Seirococcus axillaris* (Kütz.) Grev.; A, part of a fertile plant; G, diagrammatic longitudinal section through apex, *a–f* successive outgrowths, 1–7 successive growing points. B, *Axillaria constricta* (Kütz.) Gruber, part of a fertile plant. C–F, *Ascophyllum nodosum* (L.) Le Jol.; Gruber, part of a fertile plant. C, habit of a young plant; D, small part of a mature plant showing position of laterals; E, the same, with fertile laterals; F, part of an adult plant. *a*, long axis; *b*, air-bladder; *bs*, basal shoot; *d*, attaching disc; *g*, apex; *l*, outgrowths subtending *la*, lateral branches; *r*, receptacle. (C–E after Oltmanns; F after Taylor; the rest after Gruber.)

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A greater resemblance to *Fucus* is shown by the Australasian *Xiphophora* ((3) p. 202, (16), (74) p. 18, (79) p. 176, (81) p. 215, (82) pl. 53,[1] (83), (132) p. 500, (152), (306)), where the flat ribless thallus appears monopodially branched below, although the ultimate fertile parts are dichotomous. There are no air-bladders. *Axillaria constricta* (*Carpoglossum constrictum* Kütz. (197) p. 349; *Ozothallia* (*Ascophyllum*) *constricta* Ag.), a sublittoral South African seaweed, approaches nearer to *Ascophyllum* ((74) p. 17). The characteristic notches on the longer fronds (fig. 115 B, *l*) subtend vegetative laterals (*la*) or short pear-shaped receptacles (*r*); both emerge from marginal slits extended in the plane of the thallus. The essential difference from *Ascophyllum* lies in the absence of dichotomous branching, in which respect *Axillaria* agrees with several allied genera. In these, however, the principal fronds bear leafy laterals which are probably homologous with the notches of *Axillaria*.

Such forms are well illustrated by the Australian *Seirococcus axillaris* ((82) pl. 4; *Scytothalia axillaris* Kütz. (74) p. 11, (178) p. 62). The flat fronds (fig. 115 A) here bear large leafy outgrowths (*l*) arising in two alternating rows. The apex (*g*) is occupied by a rounded depression covered in by the rudiments of these laterals (fig. 115 G, *d–f*) and with the slit harbouring the apical cell (1) at its base. The leafy laterals are stated not to grow by means of an apical cell, but are formed by the division of groups of surface-cells (p. 353). Branches repeating the structure of the main axis arise at rare intervals (fig. 115 A, *la*). The small and crowded moniliform receptacles (*r*) for the most part occupy the adaxial margins of the laterals; they are simple or branched and each swelling harbours a single conceptacle, the male usually at the base, the female nearer the top ((251) p. 34).

A number of genera resemble *Seirococcus* in the possession of leafy laterals and like it are no doubt derivatives of *Fucus*-like types. In *Scytothalia dorycarpa* (Turn.) Grev. ((74) p. 15, (79) p. 456, (82) pl. 9) the prominent receptacles mainly occupy the margins of the axis between the "leaves". This is also so in *Cystosphaera* ((247) p. 146), which is distinguished by dichotomous branching and the possession of axillary vesicles. *C. Jacquinotii* is a characteristic sublittoral Antarctic species ((314) p. 47). Similar stalked air-bladders occur in *Marginariella* (*Marginaria* (79) p. 175, (81) p. 213, (130) p. 312, (271)) and, like the crowded spindle-shaped receptacles, arise from the edges of the thallus-branches. In *Phyllospora* ((3) p. 252, (74) p. 15, (81) p. 214) the numerous toothed laterals, borne on the flattened leathery axes (fig. 116 A, *l*), are narrowed basally so that there is a greater resemblance to foliar organs. The smaller receptacular branches (*r*) arising between them are often provided with a large basal air-bladder (*v*). The laterals are again devoid of an apical cell and develop without order. *P. comosa* ((82) pl. 153) is one of the largest Australian Fucoids growing in exposed situations near low-tide level. A more aberrant form is the Australian *Scaberia* ((82) pl. 164) in which the laterals are verrucose pseudo-peltate structures harbouring the conceptacles in their dilated ends and in part replaced by large globular air-bladders covered with warts.

[1] As *Fucodium gladiatum* Ag.

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The genera grouped as Fucaceae all exhibit more or less marked flattening of the greater part of the thallus, although a basal stalk is often present in older plants. The least specialised member is *Fucus*, with its essentially dichotomous branching; *Pelvetia* readily falls into line with it. In *Ascophyllum* and its allies (*Axillaria*, *Seirococcus*, etc.) there is a progressive replacement of dichotomous by monopodial

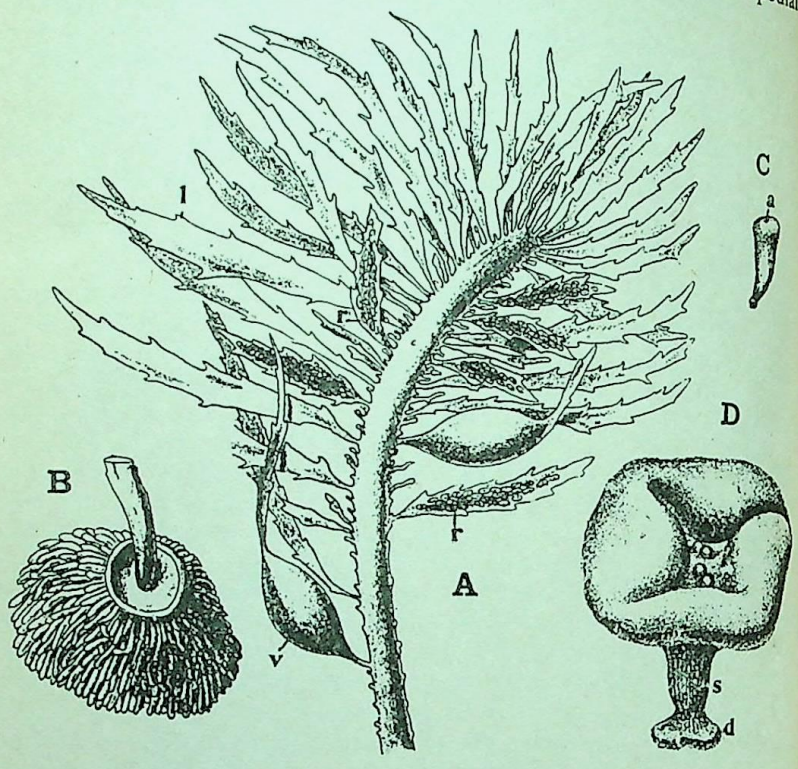

Fig. 116. A, B, *Phyllospora comosa* (Labill.) Ag.; A, part of a fertile plant; B, attachment organ. C, D, *Himanthalia lorea* (L.) Lyngb.; C, young and D, older plant. *a*, apical depression; *d*, attaching disc; *l*, lateral; *r*, receptacle; *s*, stalk; *v*, air-bladder. (A, B after Harvey from Engler-Prantl; C, D after Oltmanns.)

branching, combined with the differentiation of more or less clearly marked fertile laterals. The affinity between the diverse members of the *Ascophyllum*-alliance is evident from a comparison of the structure of the growing apices and the details of branch-development (cf. p. 353). Moreover, the mature plants of all Fucaceae so far investigated possess a four-sided apical cell, which is met with in no other representatives of the order.

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(*b*) The Genus *Himanthalia*

This striking seaweed ((70), (178) p. 66, (210) p. 13, (275) p. 48, (291)) is abundant near low-tide level on moderately exposed shores, often growing attached to steep cliff-faces (fig. 117 A). The thallus is sharply differentiated into sterile and fertile portions. The former is represented by a stalked *Peziza*-like structure (fig. 116 D), which may reach a diameter of several centimetres. The stalk (*s*), attached by the custosmary disc (*d*) and between ½ and 2 cm. in length, is somewhat flexible, so that the cup can yield to wave-action. The upper surface of the cup

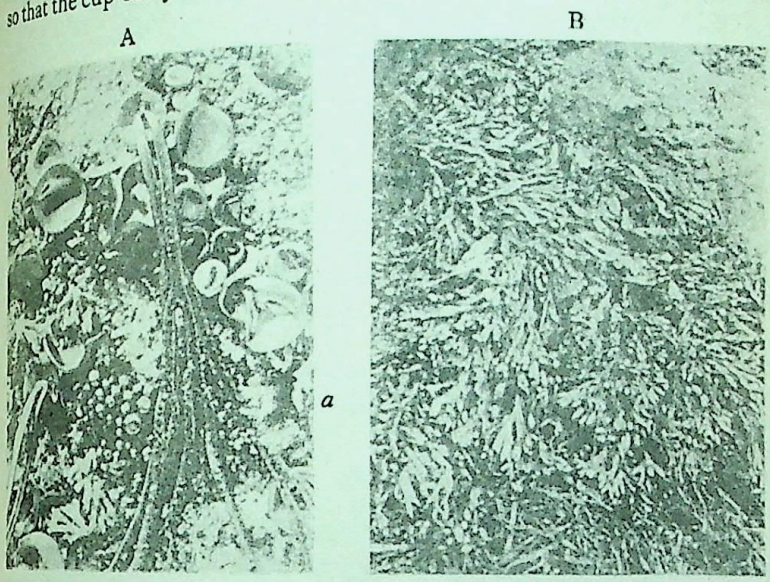

Fig. 117. A, *Himanthalia lorea* Lyngb., The Ledges, Port St Mary, Isle of Man, plants in various stages of development, the youngest at *a*; at *l* plants of *Laurencia hybrida* Lenorm. B, *Fucus vesiculosus* L. above and *Ascophyllum nodosum* (L.) Le Jol. below, on the coast of the Faeroes. (A, photo: Margery Knight; B, photo: F. Boergesen.)

is concave, and in relatively young stages a central dot (fig. 116 C, *a*) marks the position of the apical pit; in older plants 2–4 such pits can be distinguished. During the second or third year of its life from 1–4 (generally 2) long, band-shaped, dichotomously branched receptacles (fig. 117 A), bearing conceptacles throughout most of their length, grow out from the concave surface and, after liberation of the sexual cells, the whole plant usually dies away ((291) p. 532; cf. however (70) p. 16). The receptacles, though only 1–2 cm. broad, can reach a length of 2 metres; the apical slit is here orientated at right angles to the surface. A small basal part, rather narrower than the rest, is sterile and is stated ((291) p. 497) to be especially flexible. The young receptacles are negatively geotropic (36).

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Young stages of *Himanthalia* ((178) p. 68) are pear-shaped (fig. 116 C) and much like those of *Fucus*; occasional abnormal individuals retain this form permanently ((70) p. 12). Most soon broaden and become concave at the top, whilst the lower part differentiates as the stalk. The receptacles represent one fork of a dichotomy, the other limb of which remains arrested.

This rather isolated type appears to be most nearly allied to *Fucus*. The vegetative part of the plant somewhat resembles a young stage of the latter, though modified in shape and with branching suppressed until the time of production of the receptacles. On the other hand, in the restricted development of the primary axis, there is some resemblance to *Cystoseira* and other specialised forms.

(*c*) *Halidrys*, *Cystoseira*, and their Allies (Cystoseiraceae)

The series of genera now to be considered are for the most part monopodially branched and, since branching is usually copious, they often present a bushy habit (fig. 120 A). Few, if any, appear to be able to withstand much desiccation, and they are found either in deep rock-pools or in the sublittoral region. They are best represented in warmer seas. In certain genera the bulk of the branching takes place in one plane so that the thallus, as in Fucaceae, is bilaterally organised, and, since these are probably the more primitive types, they may be described first.

In *Halidrys siliquosa* ((80) pl. 66, (178) p. 44) the numerous, usually slightly flattened, branches are for the most part disposed in one plane and arise alternately from the margins of their respective parent axes (fig. 118 D). Most of the lower laterals develop into long shoots, some of which may reach the same length as the main axis. At higher levels the few long branches are scattered quite irregularly among the many short ones, some of which appear as mere teeth (2–3 mm. long). Certain laterals develop into characteristic, chambered and mucronate air-bladders (fig. 118 D, *b*) resembling a septate siliqua, while some of the upper ones differentiate into stalked receptacles (*r*) which are often grouped in a racemose manner. According to Reinke ((197) p. 356) many of the short branches are shed at the end of the season. In *H. dioica* ((49), (65) p. 323) flattening of the thallus is more marked.

Bifurcaria (*Pycnophycus*) *tuberculata* ((10) p. 112, (74) p. 21, (80) pl. 89, (191), (275) p. 50), frequent on the Atlantic shores of Europe and Africa, is exceptional among Fucales in possessing a richly branched, perennial rhizome attached to the substratum by small adhesive discs (fig. 118 A, *rh*). A similar rhizome is found in the South African *B. sisymbrioides* Kütz. ((197) p. 355). That of *B. tuberculata* (fig. 118 C) is a gnarled structure with numerous short, irregularly swollen branches, many of which remain arrested; these show the apical depression (*a*) very clearly. Other branches (*e*) bend up and give rise

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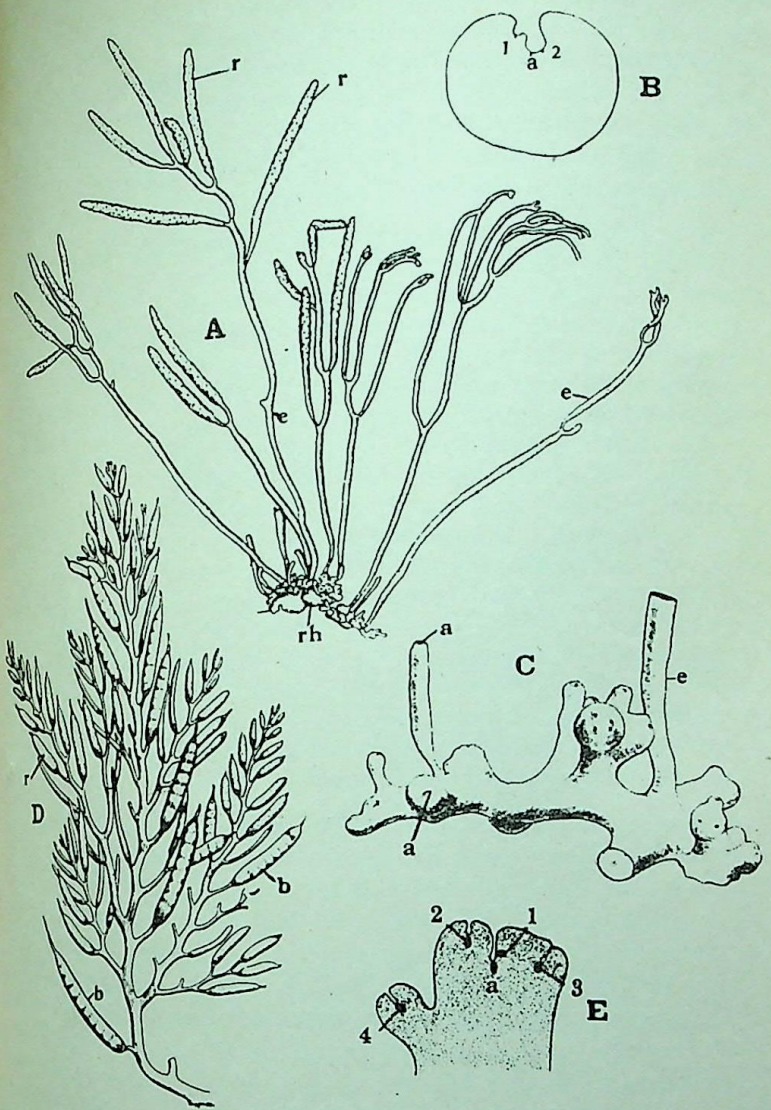

Fig. 118. A–C, *Bifurcaria tuberculata* Stackh.; A, habit of a fertile plant; B, longitudinal section of apex; C, part of rhizome enlarged. D, E, *Halidrys siliquosa* (L.) Lyngb.; D, habit of a fertile plant; E, diagrammatic longitudinal section of a branching apex, 1–4 the successive apical cells. *a*, apical cell; *b*, air-bladder; *e*, erect shoots; *r*, receptacle; *rh*, rhizome. (A after Rees; B, C after Gruber; D after Newton; E after Oltmanns.)

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to forked, terete shoots which grow to a height of 30–45 cm. (fig. 118 A) and die down in the late autumn; constrictions occur at the points of branching and where the erect axes arise from the rhizome. Despite the apparent forking the branching is, according to Gruber, actually monopodial and bilateral.

The rhizome is probably a lateral outgrowth from the axis of the young plant, which is no doubt erect and radial as in other Fucales. The tuberculate receptacles (fig. 118 A, *r*), which are often exposed at low water, arise at the tips of the upright shoots, the branches bearing them sometimes developing air-bladders.

The South African *B. laevigata* Kütz., which has a discoid holdfast and differs in other respects ((191) p. 108, (305)), has recently been referred to a distinct genus, *Bifurcariopsis* ((307) p. 211).

Brief mention may be made of certain distinctive Australasian genera. *Carpoglossum*, in the restricted sense adopted by Gruber ((74) p. 23),[1] comprises only *C. confluens* ((82) pl. 159; fig. 119 A), which is clearly less specialised than *Halidrys*. The mode of branching of the broad elongate fronds is similar, but no special receptacles are differentiated, the conceptacles merely occupying the ultimate laterals (*r*).

Greater differentiation is evident in *Platythalia* ((74) p. 24). In *P. quercifolia* (fig. 119 D; *Carpoglossum quercifolium* J. Ag. (82) pl. 43) the laterals of limited growth are foliar with serrate or almost pinnate margins and a narrowed base; some are sterile, others harbour the fertile conceptacles. The branching is bilateral, but by twisting of the axis the laterals assume a somewhat radial disposition. In the otherwise similar *Platylobium Mertensii* Kütz.[2] ((74) p. 24, (178) p. 50, (197) p. 361) special fertile shoots with marginal conceptacles arise from the edges of the leafy laterals, while large spherical air-bladders sometimes replace the receptacles or even an entire lateral.

In other Cystoseiraceae most of the branches are laid down radially from the first. This is so in *Cystoseira*,[3] several species of which occur in Britain near and below low-tide level, where they often form conspicuous submarine bushes, generally densely occupied by epiphytes. The genus is, however, more characteristic of warmer temperate and tropical seas ((58) p. 265, (233), (234) p. 82, (281) p. 135); its species form a prominent belt below low-water mark in many parts of the Mediterranean ((54) p. 210, (227), (273) p. 11, (315) p. 186). The Pacific *C. osmundacea* (Menz.) Ag. ((65) p. 333, (243) p. 709) may grow to a length of 6 metres, whilst *C. canariensis* Sauv. ((25) p. 102) reaches a height of only 14 cm. Several species show a striking iridescence

[1] *Carpoglossum constrictum* is the type of Gruber's *Axillaria* (p. 329), whilst *C. quercifolium* J. Ag. and *C. angustifolium* J. Ag. ((82) pl. 128) are referred by him to Sonder's genus *Platythalia*.

[2] This species is referred to *Cystophora* (p. 339) by some authorities ((278) p. 138). Schmidt ((235) p. 229) points out that there is a Leguminous genus *Platylobium* and proposes the name *Neoplatylobium*.

[3] See (48), (178) p. 51, (197) p. 358, (225), (227), (280).

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(120) p. 669, (223), (225) p. 146), and the majority favour well-illuminated habitats ((58) p. 265), although *C. Montagnei* J. Ag. penetrates to depths of 50 metres in the Mediterranean. Species of *Cystoseira* are occasionally attacked by a Pyrenomycetous fungus ((177) p. 3).

There is usually a distinct main axis (fig. 120 A, C, *m*), but this mostly reaches no appreciable height; it is rounded or angular in

Fig. 119. A, B, *Carpoglossum confluens* (R. Br.) Kütz.; A, part of a fertile plant; B, apex of a frond. C, D, *Platythalia quercifolia* (R. Br.) Sond.; C, apex of a growing frond; D, part of a plant. *a*, apical depression; *r*, receptacle. (After Gruber.)

cross-section and attached by a basal disc (*d*) which is often somewhat conical. In a few species (e.g. *C. Abies-marina* C. Ag.) the main axis is prostrate, whilst in *C. fibrosa* C. Ag. it is elongate and flattened and bears distichous branches. As a general rule, however, the primary laterals are disposed in a 2/5 spiral and grow to a much greater length than the main axis, which may be altogether hidden among them (e.g. *C. granulata* ((80) pl. 60). Its height is given as 1–2 cm. in *C. amentacea*, 1–10 cm. in *C. abrotanifolia* (fig. 121 C), 10–30 cm. in *C. crinita*, and

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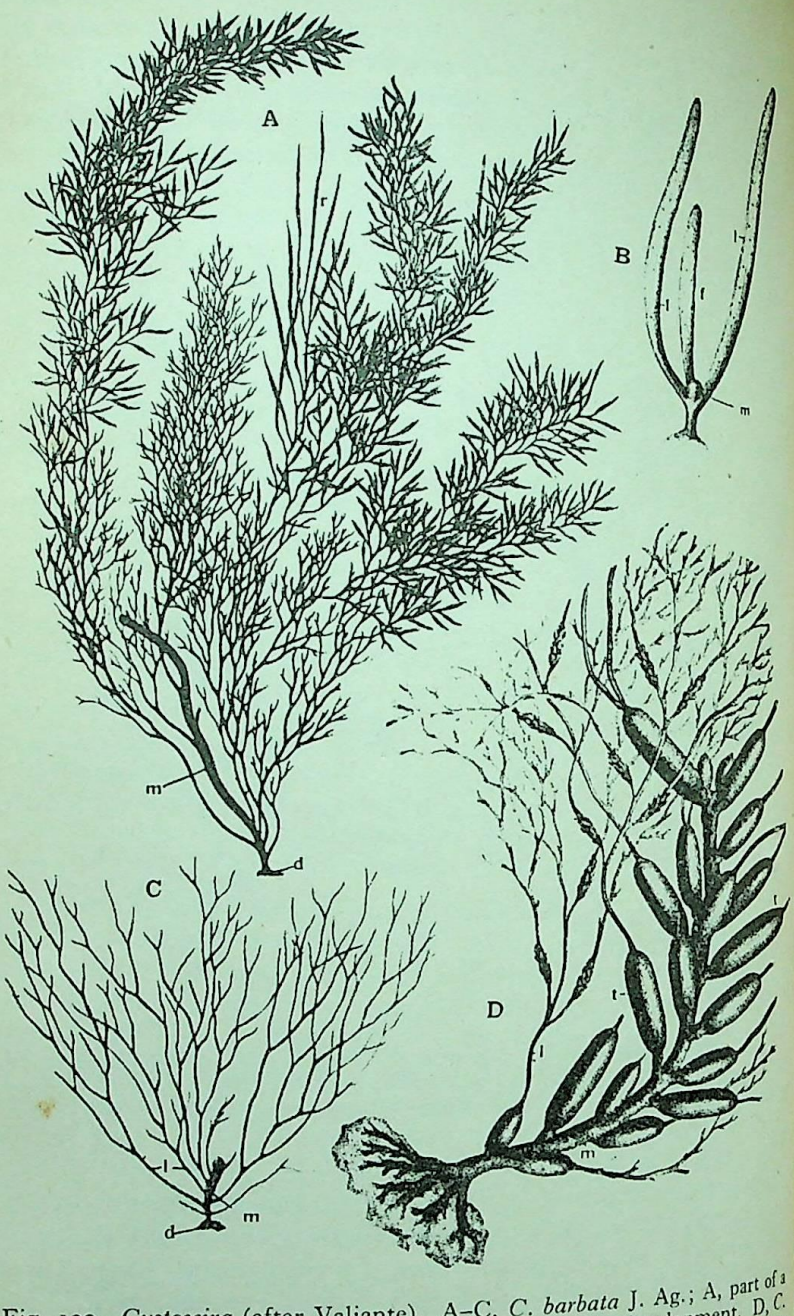

Fig. 120. *Cystoseira* (after Valiante). A–C, *C. barbata* J. Ag.; A, part of a mature and fertile plant; B, early and C, later stage in development. D, *C. opuntioides* Bory, lower part of a plant. *d*, attaching disc; *f*, primary axis; *l*, lateral; *m*, definitive axis; *r*, receptacle; *t*, dilated base of lateral.

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60–75 cm. in *C. barbata*. The full height is only gradually attained, the annual growth being small.

The laterals always show extensive monopodial branching. In some species the ultimate ones are very short so that the habit is ericoid (*C. ericoides* Ag. ((80) pl. 265). In others (*C. abrotanifolia*, *C. osmundacea*, etc.) the basal parts of the primary laterals, and sometimes of those of higher orders, are flat and more or less markedly lobed, with all the branches arising in one plane (cf. also (178) p. 49).[1] The young plants then present a characteristic appearance (fig. 121), altogether different from that of the mature stage, in which the primary laterals and their branches have lengthened, become terete, and acquired the normal radial branching. In most species, however, all the branches are terete and radial from the first (fig. 120 A, C). Air-bladders (222) are commonly present and usually occupy the lower parts of the ultimate laterals, often occurring in short series. The receptacles are frequently spindle-shaped (fig. 120 A, *r*).

All *Cystoseiras* are perennial,[2] although a few are sometimes monocarpic (*C. abrotanifolia*). During the annual lengthening of the main axis it often undergoes considerable increase in thickness. On the approach of the dormant season a more or less considerable part of the branch-system is usually shed, and the plant may assume a strikingly different appearance ((221), (225) p. 146). The laterals of the first order usually develop continuously and finally become detached as a whole, leaving a stump or a mere scar on the main axis. In certain species, however, which are distinguished by the dilated bases ("tofuli" of Valiante ((280) p. 8) of the primary laterals (fig. 120 D, *t*), their development takes place in two stages ((225) p. 143), the swollen bases arising towards the end of the period of active growth and remaining dormant until the following season when they grow out into branches. The basal dilation persists after the upper part of the branch is shed. In some species (*C. Montagnei* J. Ag., *C. spinosa* Sauv.) all the primary laterals develop in this way, and the surface of the main axis becomes covered with an uninterrupted series of tubercles (fig. 120 D), but in others (*C. granulata*, *C. platyclada* Sauv.) some of the first-formed primary laterals of each season lack the basal dilation. The axis then bears alternating series of tubercles and scars by means of which its age can be determined ((225) p. 144).

Shedding of the branches occurs both in littoral and sublittoral species, but does not take place in young plants. In the new season branches in the tuberculate forms arise not only from the apical tubercles, but also adventitiously from the swollen bases of older laterals. In certain species the long laterals, after they are shed, are replaced by numerous short branches (*C. mediterranea* (Ag.) Sauv.) or, as in *C.*

[1] As *Halidrys osmundacea*.

[2] These data are based on Sauvageau's extensive observations in the Mediterranean and adjacent seas.

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foeniculacea ((80) pl. 122, (225) p. 146), by flattened shoots with distichous laterals, devoid of air-bladders.

The tubercles are probably storage-organs. They consist of thin-walled cells, are devoid of hyphae, and are traversed by a central strand of elongate cells. They are commonly covered with spiny outgrowths which also often occur abundantly on other parts of the thallus.

The young plants ((280) p. 3) resemble those of *Fucus*, especially in species like *C. abrotanifolia* in which the upper part of the embryo flattens at an early stage (fig. 121 A, *f*), but so far as present evidence goes, the primary axis of the embryo does not develop beyond a certain stage. When it has reached a length of 5 or 6 mm., an apical cell arises near its base (*d*) and soon becomes sunk in the usual depression ((280) p. 6). The active division of this apical results in the

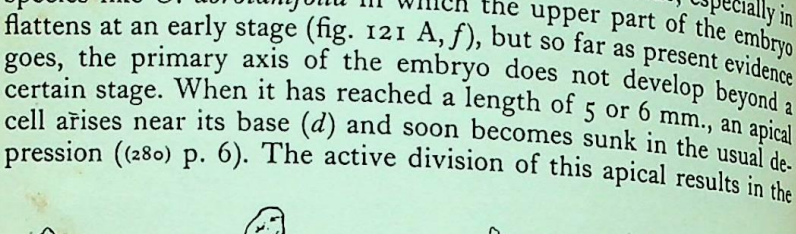

Fig. 121. *Cystoseira abrotanifolia* C. Ag., three successive stages in development (after Valiante). A, young embryo; B, older embryo showing primary frond (*f*), the definitive axis (*d*) and two laterals (1, 2) developed from it; C, a young plant. *a*, attaching disc; *d*, definitive axis; *f*, primary axis; *l*, lateral; *m*, main axis; *p*, stalk.

production of a secondary shoot (fig. 121 B, *d*) which becomes the definitive axis of the plant and, as the latter becomes established, the primary axis (*f*) above its place of origin is gradually turned to one side. The basal part of the axis is therefore a sympodium. All the later laterals, however, develop monopodially and in acropetal succession from the definitive axis (fig. 121 C) which persists throughout the life of the plant. The first two laterals (fig. 120 B) arise on opposite sides of the axis, and it is only after this that a 2/5 divergence is established, although subsequent displacement causes the first two laterals to fall into the 2/5 spiral. The early development has only been examined in a few species, and it remains to be seen whether the sequence just outlined is always followed.

In certain species (*C. foeniculacea*, *C. abrotanifolia*) several fronds arise from the basal disc in the older plant. This is due ((225) p. 142) to the development of adventitious branches from the lower part of the axis, which gradually become incorporated in the enlarging holdfast.

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The large genus *Cystophyllum*, widely distributed in Japanese waters ((299)), has the habit of a *Cystoseira* and the two genera are no doubt nearly allied. It is not easy to draw a sharp distinction between the mature plants of the two genera. According to Yendo ((299) p. 35) the only general difference lies in the restriction of air-bladders to the ultimate branchlets in *Cystophyllum* (cf. (82) pl. 139). Another imperfectly known genus of this affinity is the Australasian *Cystophora*[1] ((7) p. 44, (81) p. 214, (82) pl. 175, (302)), which is chiefly distinguished by its stalked air-bladders. In some species the entire vegetative system is bilateral, the fertile branches alone showing a radial arrangement.

A rather different type is seen in *Landsburgia* ((74) p. 28, (81) p. 213), where the almost terete main axes bear radially disposed laterals, some of which resemble the axis, while others develop as lobed leafy structures (fig. 123 A); smaller laterals of the latter type (*r*) harbour the conceptacles. There is some resemblance to *Platythalia* (p. 334). The leafy laterals of *Landsburgia* recall those of the young plants of such *Cystoseiras* as *C. abrotanifolia*, and there is also similarity to the flat basal parts of the primary laterals of certain *Cystoseiras*. Oltmanns ((179) p. 199) may well be right in looking upon *Landsburgia* as a relatively primitive representative of the radial Cystoseiraceae, although Gruber regarded it as a specialised form.

The radial organisation of *Cystoseira* and its allies is probably secondary, and there is reason to believe that bilateral forms like *Halidrys* represent the more primitive condition within the family. Their derivation from *Fucus*-like types presents no difficulty. It may be recalled that some *Cystoseiras* retain a bilateral organisation in the early branching of their primary laterals. All Cystoseiraceae appear to possess a three-sided apical cell (p. 353).

(*d*) *Sargassum* and its Allies (Sargassaceae)

The genera included in the Sargassaceae,[2] which are in part rather vaguely defined, exhibit the most complex morphology among Fucales. Like the Cystoseiraceae some show bilateral, others radial organisation, and the former are no doubt more primitive. The branching is always monopodial. All the members of the family are distinguished by the special features of the lateral branch-systems. These (figs. 122 A, F, H; 123 C) bear at their base one or two leaf-like organs (*l*), in the "axil" of one of which the whole system often appears to arise. The three-sided apical cell is lodged at the base of a deep funnel-shaped depression. Species of *Sargassum* are not native to Britain, although *S. natans* (*S. bacciferum* Ag. (80) pl. 109) is sometimes cast up after storms. A few (*S. Hornschuchii* Ag., *S. linifolium*) occur in the Mediterranean, but the main centre of

[1] Incl. *Blossevillea* ((9) p. 336, (197) p. 362; cf. however (235) p. 230).

[2] For the general literature of *Sargassum*, see (5), (7) p. 49, (75), (194*a*), (195), (238–42), (299).

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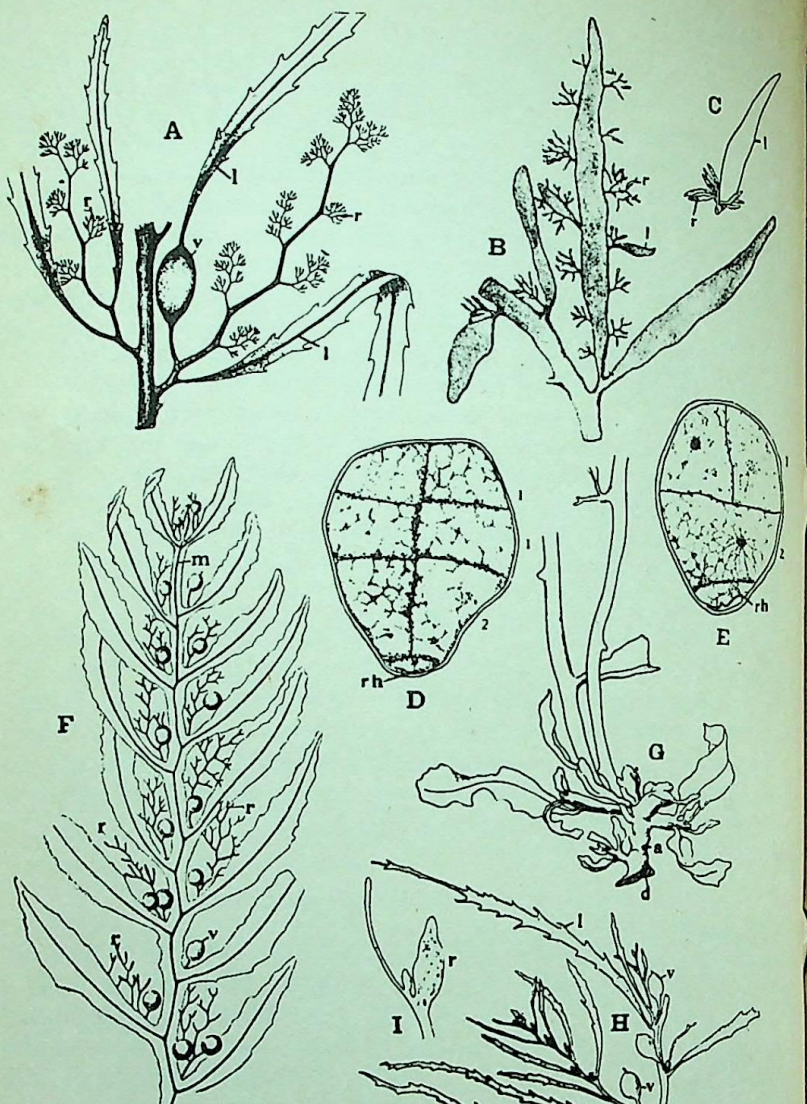

Fig. 122. A, *Sargassum* (*Anthophycus*) *longifolium* Ag., small part of a fertile plant. B, C, *Carpophyllum flexuosum* (Esp.) Grev.; B, part of a fertile plant; C, lateral with axillary cluster of receptacles. D, E, *Sargassum linifolium* (Turn.) Ag., young embryos, *1*, *2* the two primary cells. F, *S.* (*Pterocaulon*) *Peronii* (Mert.) C. Ag., part of a fertile plant. G, *S. Vachellianum* Grev., basal part of a plant. H, I, *S. enerve* C. Ag. *a*, main axis; *d*, attaching disc; *l*, lateral; *r*, receptacle; *rh*, rhizoid-cell; *v*, air-bladder. (A, F after Kützing from Oltmanns; B after Gruber; C after Dawson; D, E after Nienburg; G–I after Setchell.)

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distribution is in the Southern Hemisphere and especially in the warmer seas (see map 2, p. 252; and (241*a*) p. 574, (281) p. 135).

With Oltmanns ((178) p. 61, (179) p. 202) the South African *Sargassum* (*Anthophycus*) *longifolium* may be taken first as representing a relatively unspecialised type. The lateral branch-systems here show a distichous arrangement throughout the plant. On the lower parts of the long axes they are represented merely by leafy outgrowths flattened in the plane of branching, but above they constitute fertile systems comprising a number of distinct structures (fig. 122 A). Near the base these bear two alternate "leaves" (*l*) which are again expanded in the plane of branching; the upper adaxial one usually surmounts a prominent air-bladder (*v*) which is occasionally alone present. Beyond this the axis of the lateral bears a series of repeatedly branched receptacles (*r*). In several of the distichous species (e.g. *S. Peronii* fig. 122 F; (4) p. 54, (178) p. 62, (197) p. 365) both the axes and the laterals are flattened, and a midrib (*m*) may be present throughout. Agardh ((5) p. 3) regarded such species as primitive.

From forms like these there are many gradations to the typical *Sargassums* (Sect. *Eusargassum*) which are radially organised and present a bushy habit like that of a *Cystoseira*. As in that genus, too, the main axis is commonly only a few centimetres high (fig. 122 G, *a*), and it is the richly branched primary laterals that constitute the greater part of the vegetative system. The *Eusargassums* comprise about two-thirds of the known species and are essentially confined to tropical seas. In them the terete or angular branches of the first and higher orders are spirally arranged and bear numerous laterals of limited growth (figs. 122 H; 123 C), in which the basal "leaf" (*l*) is usually the most conspicuous. These foliar organs, which are sometimes very narrow (e.g. *S. patens* Ag.), commonly possess a serrate margin and are usually provided with an obvious midrib (absent in *S. enerve*, fig. 122 H). In certain species the long axes bear wart-like outgrowths giving them a spiny or verrucose appearance. Parts of the branch-system may be shed periodically and later replaced by new growth ((259) p. 212).

Both the primary and the subsidiary branch-systems develop a basal "leaf" which more or less clearly subtends the remainder of the branch-system (figs. 122 H; 123 C). The "leaves" (*l*) are, as a general rule, flattened in the vertical plane, although commonly expanded horizontally in the lower parts and sometimes over a considerable part of the plant ((240) p. 2), for the most part probably as a result of twisting of their stalks ((5) p. 5). On the lower parts of the long shoots some of the laterals comprise little but this leaf, although there are sometimes axillary rudiments, but in the upper regions of mature plants many of the "leaves" subtend axillary branch-systems (fig. 123 C), which appear condensed as compared with those of *Anthophycus*. The lowest member or members of these branch-systems usually develop

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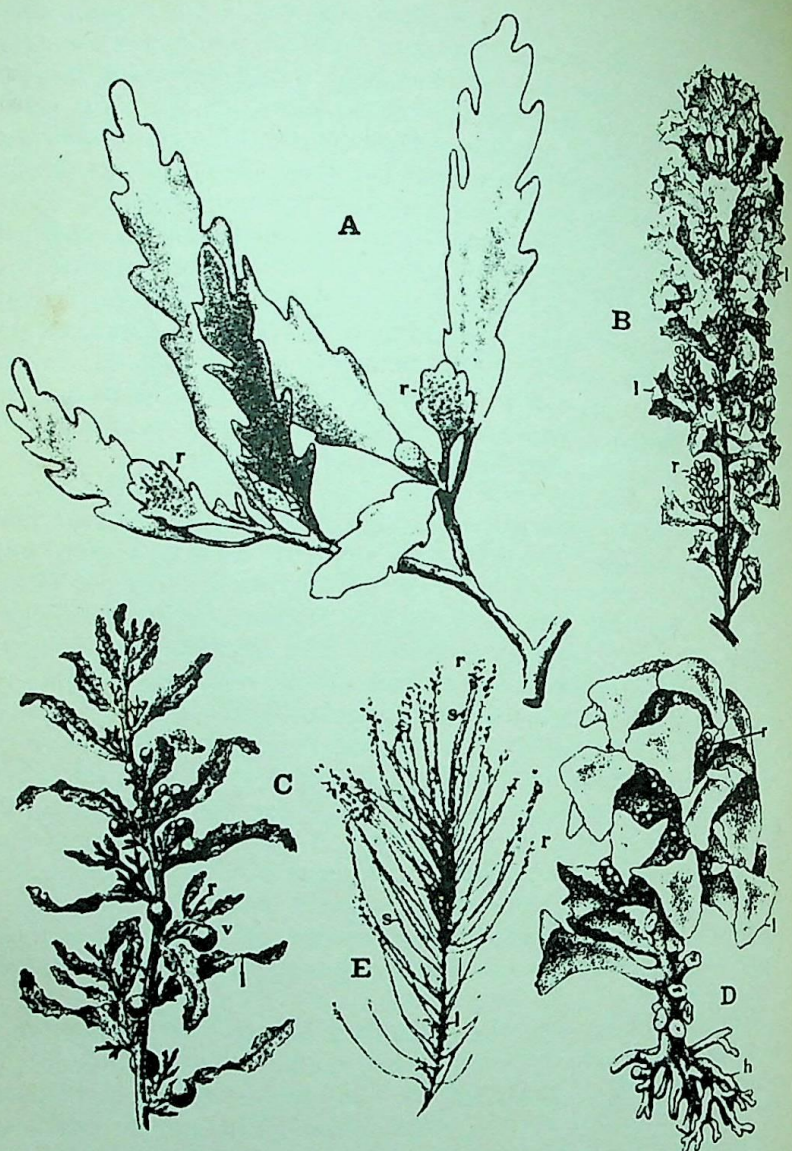

Fig. 123. A, *Landsburgia quercifolia* Hook. & Harv., small part of a fertile plant. B, *Turbinaria dentata* Barton, ditto. C, *Sargassum vulgare* Ag., ditto. D, *Turbinaria Murrayana* Barton. E, *Coccophora Langsdorfii* (Turn.) Grev., fertile plant. *h*, hapteron; *l*, lateral; *r*, receptacle; *s* (in E), scales; *v*, air-bladder. (A after Gruber; B, D after Barton; C after Boergesen; E after Okamura & Oshima.)

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as stalked air-bladders (*v*) which may or may not be crowned by a leafy termination; the extremes are seen in fig. 122 A and H. Not uncommonly, however, the lowest member may develop as a leaf, while conversely the subtending leaves are sometimes replaced by air-bladders; the latter are no doubt homologous with the "leaves". The subsequent members of the axillary branch-systems, which are more or less richly branched, are cylindrical or flattened and constitute the receptacles (figs. 122 I; 123 C, *r*). While it is convenient to speak of "leaves" and "axillary branches", the whole lateral no doubt represents a single branch-system, the first member of which appears as the subtending leaf (cf. p. 353).

This brief account is inadequate to afford a true conception of the range of form which is presented by the species of *Sargassum* and which will be evident from a perusal of the works cited in the bibliography. The lateral branch-systems exhibit a varied differentiation, both in different individuals and in different species. In *Acystis* (230), recorded from the Red Sea, the erect shoots arise from a prostrate and flattened rhizome and there are no air-bladders.

Certain bilateral flattened forms, devoid of air-bladders on the axillary systems (fig. 122 C) and characterised by the possession of an elongate main axis, are usually referred to a separate genus *Carpophyllum* ((41), (45), (178) p. 61), well represented in the Australasian region. Judging by Gruber's figure (fig. 122 B) the subtending leaf is sometimes suppressed, the branched receptacles (*r*) then arising direct from the margins of the flattened shoots. These forms possibly constitute a distinct evolutionary line.

In *Turbinaria* ((15), (82) pl. 131) the radially organised plants are compact and cone-like. The laterals take the form of firm, more or less peltate structures (fig. 123 B, D, *l*) bearing the short well-branched receptacles (*r*) in clusters on the upper sides of their stalks. Certain species possess a conspicuous air-bladder below the peltate enlargement, while in *T. trialata*, for example, the stalk is winged. Attachment is effected by a system of spreading branches at the base of the main axis (fig. 123 D, *h*).

The monotypic *Coccophora*[1] ((3) p. 249, (74) p. 26, (175), (252), (299) pl. 5) has a perennial basal disc from which long shoots arise in each season. At the beginning and towards the end of their growth they produce dichotomously branched filiform laterals (fig. 123 E, *l*), but over most of the older part they bear triangular scale-like appendages. Axillary systems that bear secondary filiform laterals appear sooner or later, but on the lower parts of the axes these laterals remain small, while on the upper many of them lengthen and branch extensively so that the shoots assume a densely tufted appearance. More than a year after the appearance of the long shoots, the upper axillary systems undergo marked elongation (fig. 123 E), producing scales (*s*) similar to those borne on

[1] *C. imperata* Yendo ((299) p. 53) has been shown to be merely a young stage of *C. Langsdorfii*, while *C. phyllamphora* J. Ag. is only a form of the latter ((299) p. 49).

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the main axis and, after some time, developing at their tips a number of stalked rounded receptacles (*r*); soon after this the whole shoot dies. No clear information is available as to the relation between the axillary systems and the filiform laterals from which they arise, but *Coccophora* would appear to be one of the most highly specialised members of the order.

(*e*) Hormosiraceae

All the Fucales hitherto noticed possess a single apical cell, but the Australasian genera *Hormosira* and *Notheia*, although they resemble the others in many respects, differ in the presence of several apical cells (p. 354). Oltmanns classes them as *Anomalae*, but they are perhaps better considered as constituting a separate family.

Hormosira ((69), (74) p. 4, (82) pl. 135, (151)) is a plant of characteristic habit (fig. 124 C), the dichotomously branched thalli consisting of much enlarged hollow segments (*v*) separated by short solid stalks (*s*). Sterile and fertile conceptacles (fig. 124 D, *c*) are irregularly scattered over the vesicular segments. In transverse sections through base or apex of the latter the central hollow is produced into four (rarely three) bays, but towards the middle of the segment these disappear and there is a wide cavity bounded by a large-celled tissue penetrated by hyphae.

Notheia ((17), (74) p. 6, (82) pl. 213, (130), (150)) is a small epiphyte about 12 cm. high, so far only found on *Hormosira* (figs. 124 B; 133 E) and *Xiphophora*. The terete thallus is branched monopodially and bears conceptacles throughout. The branching is peculiar (fig. 124 E) in the fact that the laterals (*l*) arise from the bases of the conceptacles which at the same time also harbour oogonia ((150), (293) p. 635) or antheridia ((17) p. 421). According to Barton ((17) p. 423) the zygote gives rise to a septate filament which penetrates between the cells of the host and branches profusely; in the older plant ((293) p. 637) the endophytic portion consists of a mass of elongate colourless cells. In segments of *Hormosira* occupied by *Notheia* the central hollow is filled by proliferation of the medulla.

The relation of these two genera to other Fucales is not at present clear.

(*f*) Durvilleaceae

Durvillea, a striking member of the vegetation of the Subantarctic seas (*D*, map 2, p. 252), presents many resemblances to one of the larger *Laminarias* (fig. 124 A). In *D. antarctica* (*D. utilis* Bory)[1] the circular attaching disc (*a*) may be more than half a metre in diameter and bears several fronds which may reach a length of 10 metres. The

[1] See (9) p. 340, (61) p. 51, (72) p. 610, (74) p. 3, (79) p. 454, (87), (187) pl. 1, (247) p. 140, (248) p. 52, (314) p. 48.

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relatively short stipe (*st*), which increases in thickness year by year and may become 7·5 cm. thick, is flattened at its upper end, where it passes over gradually into the leathery blade. The latter divides into

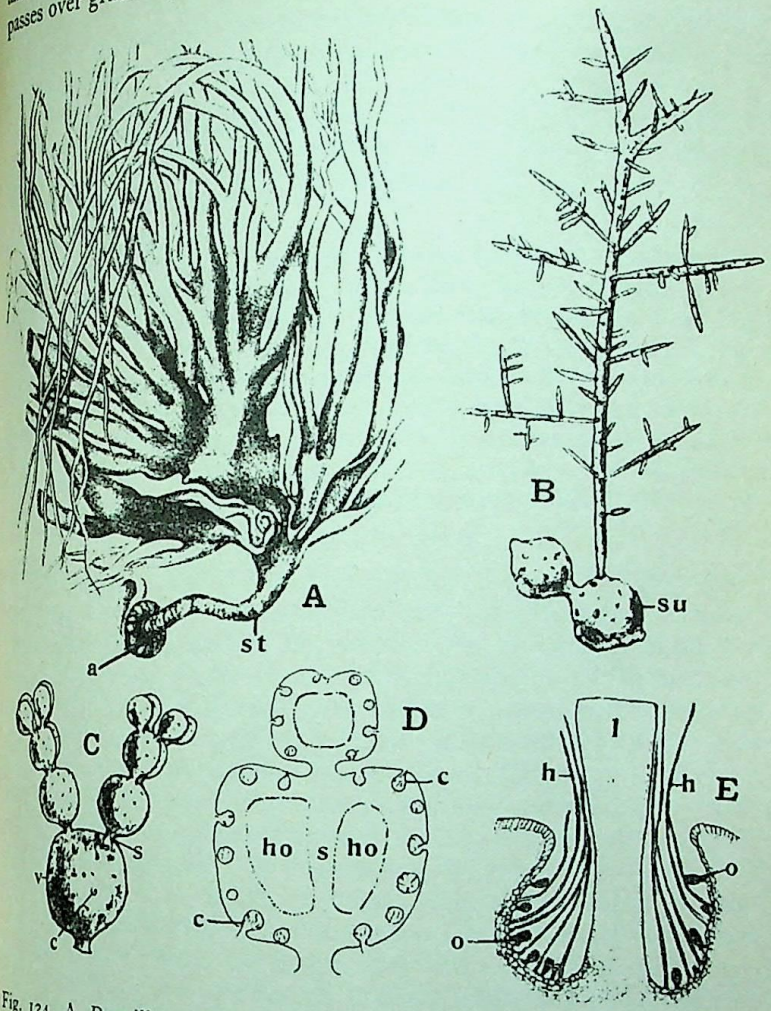

Fig. 124. A, *Durvillea antarctica* (Cham.) Hariot. B, E, *Notheia anomala* Bail. & Harv.; B, a plant epiphytic on *Hormosira*; E, vertical section through a female conceptacle, with a lateral branch. C, D, *Hormosira Banksii* (Turn.) Decsne; C, habit of a small plant; D, longitudinal section through two segments. *a*, attaching disc; *c*, conceptacle; *h*, hair; *ho*, cavity; *l*, lateral; *o*, oogonium; *s*, solid tissue; *st*, stipe; *su*, substratum; *v*, hollow segment. (A after Postels & Ruprecht; the rest after Gruber.)

numerous narrow whip-like segments, in which the central tissue breaks down with the formation of a number of chambers which become inflated with gases. *D. antarctica* is an inhabitant of the littoral zone, but favours localities where there is strong wave-action so that

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it is always covered with spray. Where the growth is luxuriant, the segments of the blades become densely tangled ((247) p. 141). *D. Harveyi* is considerably smaller and the undivided portion of the blade is more extensive.[1]

Durvillea possesses neither an apical, nor an intercalary meristem and growth is diffuse. The segments of the blade are stated to arise as local outgrowths. Despite the *Laminaria*-like habit, fertile conceptacles differing only in minor particulars from those of other Fucales are scattered over the whole thallus. On the whole, therefore, the resemblances to Fucales are greater than those to Laminariales.

Skottsberg's *Ascoseira* ((247) p. 148, (248) p. 50), referred to a distinct family, has a repeatedly forked stipe, each branch of which terminates in a long and rather narrow, leathery blade, bearing conceptacles on both surfaces except in the basal portion. The conceptacles contain chains of reproductive organs, each producing eight reproductive cells of unknown nature. The relation to other Fucales remains quite obscure (cf. also (129) p. 312).

EARLY DEVELOPMENT, APICAL GROWTH, AND BRANCHING

The early development of the embryo, which is known in many genera,[2] commences with rapid division of the zygote (figs. 114 G; 122 D, E; 125 A) to form a spherical or pear-shaped mass of cells attached to the substratum by more or less numerous unicellular rhizoids arising from the basal cells. Periclinal division sets in at an early stage. The first wall, dividing the zygote into an upper and a lower cell (fig. 122 E, *1*, *2*), is usually followed by a further horizontal division in the latter, whereby a small rhizoid-cell (*rh*) is cut out at the base. At the same time or soon afterwards vertical division into quadrants (fig. 122 D, E) takes place in the upper (*1*) and subsequently in the underlying (*2*) cell ((162) p. 178, (264) p. 10), while at an early stage the upper cell usually divides transversely into two tiers (fig. 122 D). The base of the zygote sometimes lengthens into a rhizoid before the rhizoid-cell is cut off ((280) p. 3), while in many Fucales the latter divides vertically into several cells before the outgrowth of rhizoids occurs; the number of cells thus produced is often considerable among Sargassaceae and varies in different species (93, 94, 173, 264, 266, 268).

In various genera the first wall is orientated at right angles to the direction of the incident light ((156) p. 139, (184), (208) p. 58, (295) p. 301) which thus determines the polarity of the plant, although this does not

[1] The genus *Sarcophycus* ((3) p. 189, (286)) is now generally included in *Durvillea* (cf. (247) p. 139).

[2] See (70), (178) p. 24, (274), (275) p. 47, (280) and the other papers cited in the text.

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apply to all Fucales; it is principally the blue rays that are concerned ((91) p. 40). The orientation of the first wall is, however, also influenced by the presence of adjacent germinating zygotes (group orientation, cf. (282) p. 303) and, where the latter are near together, light cannot overcome this stimulus. Du Buy and Olson (50) attribute this to the presence of growth regulators which are specially abundant in the ova.

The rhizoids always grow out on the side away from the light ((53) p. 640, (105) p. 685, (121), (208) p. 58). In *Fucus* it has been shown (164) that this is an effect of unequal illumination, the rhizoids appearing on the less strongly illuminated side of the zygote (cf. also (83) p. 566), and their position is not determined by the actual direction of the incident light. If zygotes are successively illuminated from two directions perpendicular to one another, the rhizoids originate between the two and lie the nearer to the first direction of illumination, the longer the light from that source has acted ((105) p. 689). Zygotes of *Cystoseira* ((104) p. 741) and *Pelvetia fastigiata* (136) subjected to centrifugal force develop rhizoids centrifugally (cf. also (309)). On the other hand Rosenvinge could recognise no effect of gravity or contact. Whitaker (284, 285) stresses the importance of gradients of hydrogen-ion concentration and suggests that this may afford an explanation of group-orientation (see also (310, 311)).

The early development of *Fucus* ((53) p. 640, (169), (178)) differs in certain respects from that of other genera. The side of the zygote away from the light grows out, usually prior to the appearance of any septa, into a rhizoid which subsequently divides to form a narrow multicellular strand (fig. 125 B, *r*). According to Nienburg ((169) p. 54) the first wall in the zygote (fig. 125 A, *1*) is followed by two other horizontal ones (*2*, *3*) giving a row of four cells; the rhizoid is largely formed from the lowest cell, although the one above contributes something. The uppermost segment divides by perpendicular walls (fig. 125 A, B, *4*), followed by horizontal segmentation (*6*) into two tiers, and then by anticlinal and periclinal walls (*7*, *9*) leading to the formation of peripheral and central cells. At the same time the underlying primary segment has subdivided (fig. 125 B) and, together with the products of the uppermost primary segment, gives rise to the body of the young plant. The prominent primary rhizoid is later supplemented by others growing out from the lower cells (fig. 125 F). A multicellular rhizoid has also been recorded in certain Japanese Fucales (95).

The subsequent development of the embryo probably always takes place in essentially the same way. Sooner or later there is abundant anticlinal division in the peripheral cells, whilst the inner ones enlarge without much segmentation (fig. 125 C). The embryo is now assuming an elongate form (fig. 125 F). Occasional periclinal divisions (fig. 125 E), whereby the number of central cells is increased, also take place in the peripheral layer (*me*) in the upper part of the embryo.

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As a result, the latter widens (cf. fig. 114 B), but the lower part remains narrow and constitutes a short stalk.

At this stage, amid the group of cells occupying the apex of the embryo of *Fucus*, one develops a specially conspicuous nucleus; this

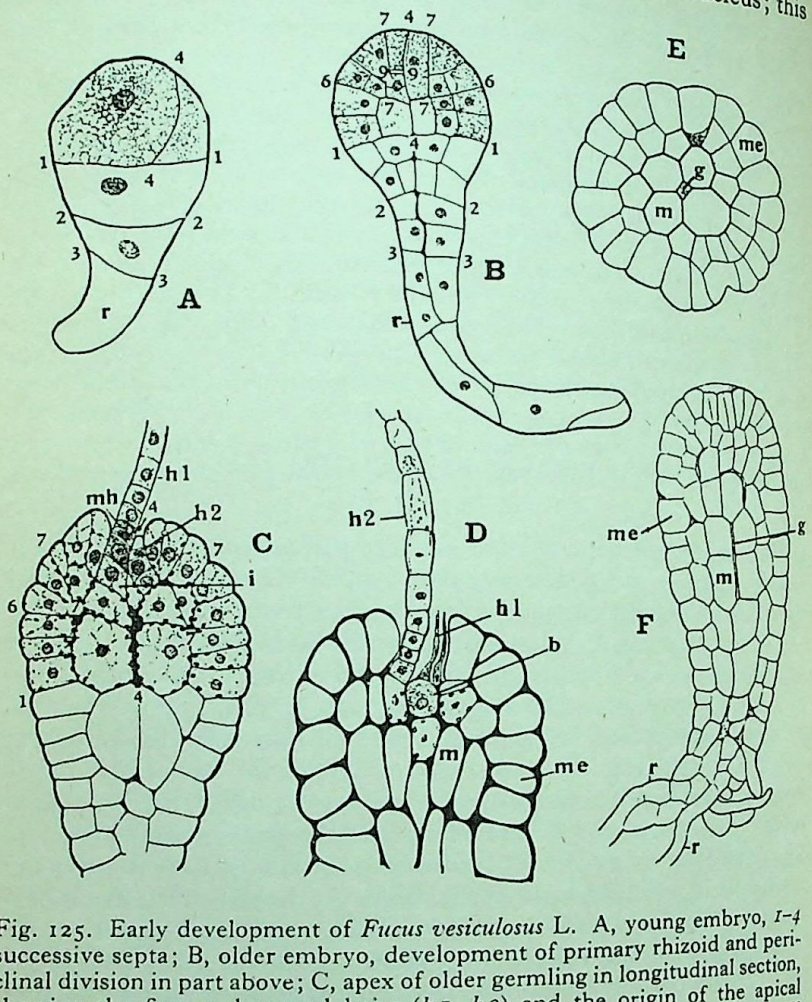

Fig. 125. Early development of *Fucus vesiculosus* L. A, young embryo, *1–4* successive septa; B, older embryo, development of primary rhizoid and periclinal division in part above; C, apex of older germling in longitudinal section, showing the first and second hairs (*h1*, *h2*) and the origin of the apical depression, the numerals in B and C the successive septa; D, apex at a still later stage, only basal cell of first hair (*h1*) surviving; E, transverse and F, longitudinal sections of germlings. *b*, basal cell of first hair; *g*, mucilaginous wall; *h*, hair; *i*, initial cell of hair; *m*, medulla; *me*, meristoderm; *mh*, meristem of hair; *r*, rhizoid. (A–D after Nienburg; E, F after Oltmanns.)

cell grows out into a first hair (fig. 125 C, *h1*; (167), (169) p. 54, (210) p. 4). As it lengthens, a meristem (*mh*) appears above the initial cell (*i*) which persists unaltered during the subsequent course of events. As the hair differentiates, the surrounding cells separate from it and

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initiate a funnel-shaped apical depression which rapidly widens (fig. 125 D), in part no doubt owing to active division of the neighbouring cells. By degrees other adjoining cells successively grow out into hairs (fig. 125 C, D, *h2*) giving the apical tuft mentioned on p. 324 (fig. 114 B). The first-formed hair (fig. 125 D, *h1*) soon disorganises, except for its basal cell (*b*) and from this, according to Nienburg, the apical cell of the young embryo is constituted. The origin of the apical cell below a trichothallic meristem recalls the condition met with in certain Ectocarpales (pp. 90, 114). It is not at present known whether such an origin is traceable also in other Fucales. Hairs have not been observed at the apex of the young embryos of *Pelvetia* ((178) p. 24) and *Ascophyllum* inter alia.

Whatever be its mode of origin in other Fucales, all who have studied the young plants record the appearance of a three-sided meristematic cell (fig. 127 I, *a*) in the apical depression at a certain stage; in longitudinal section it appears more or less biconvex (figs. 126 A; 127 H, *a*; cf. however (41) p. 286). Except in Fucaceae, this apical cell functions throughout the life of the plant. The segments (figs. 126 A; 127 G, *s*) cut off from its three faces undergo periclinal division, the outer cells becoming part of the peripheral layer, the inner ones dividing further to form the internal tissue of the embryo. For a time hairs with a basal meristem (fig. 126 A, *h*) are produced from the peripheral cells in *Fucus* but, when they have been carried on to the edge of the apical depression (fig. 126 B) as a result of the apical activity, they are usually shed. Production of hairs ceases before the apical cell has been long established.

Soon after the formation of the apical depression the greater part of the embryo of *Fucus* begins to flatten, only the basal third retaining a cylindrical form. In the flattened part a midrib soon appears, while cryptoblasts develop along the margins. At the same time the depression becomes a slit extended in the plane of flattening, the sides of the slit adjacent to the thallus-surfaces sloping steeply (fig. 126 C), whilst the marginal parts do so more gradually (fig. 126 B). It is at this stage that, in Fucaceae, the three-sided is replaced by a four-sided apical cell ((178) p. 13, (210) p. 6, (297)).[1] The latter (fig. 126 B, *a*; F) has the shape of a truncated pyramid, the rectangular base of which is directed inwards and the somewhat convex apex outwards; the lateral faces are slightly arched and of unequal size (fig. 126 D), those parallel to the plane of flattening being narrower than those at right angles to it. The distinctive shape is specially well seen in *Pelvetia* ((89) p. 32, (111), (178) p. 28) and *Ascophyllum*. It is probable that this definitive apical cell arises from the three-sided one of the embryo by

[1] Apart from the Fucaceae dealt with below, a four-sided apical cell has also been recorded in *Pelvetia fastigiata* ((155) p. 423) and *Xiphophora* ((83) p. 564, (306) p. 52). The change from a three-sided to a four-sided apical cell takes place also in adventitious shoots ((166) p. 179).

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longitudinal division ((166) p. 179, (178) p. 13). It is well protected within the apical slit which is filled with mucilage ((178) p. 19, (191) p. 110).

In *Fucus* segments are cut off successively (fig. 126 F) parallel to the base (*bs*), to the two narrower faces (*ss*), and then to one (some-

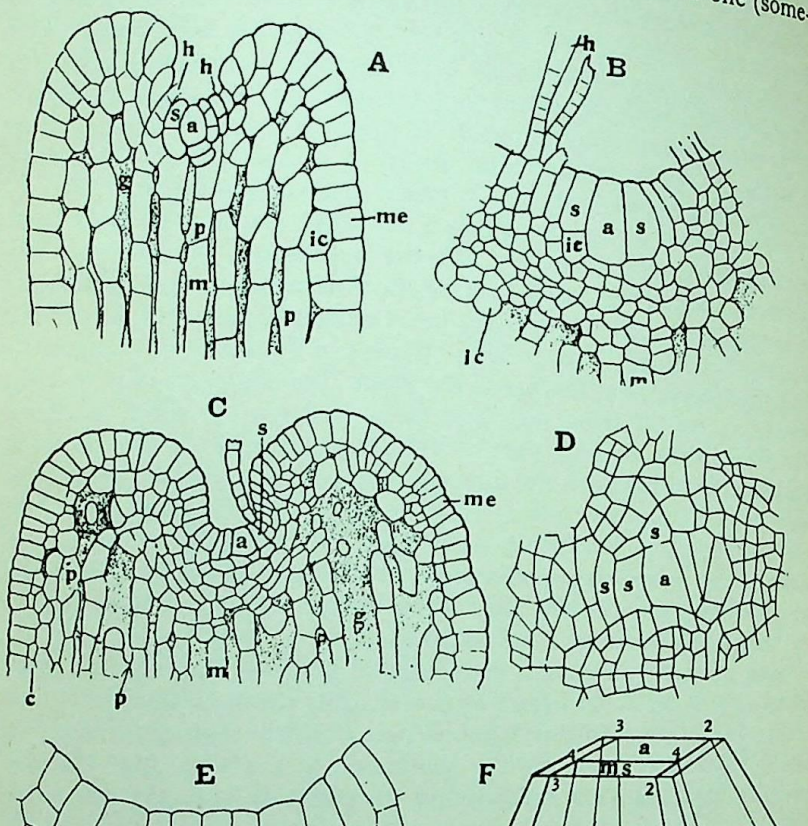

Fig. 126. Apical cell of *Fucus* (D, *F. furcatus* Ag., the rest *F. vesiculosus* L.). A, median longitudinal section of a young cylindrical germling, still with the three-sided apical cell (*a*); B, ditto of an older germling, in the plane of flattening; C, ditto, in a plane at right angles to that of flattening; D, transverse section through an older apex; E, longitudinal section of apex of a dichotomising frond; F, diagram of apical cell. *a*, apical cell; *bs*, basal segment; *c*, cortex; *g*, mucilage; *h*, hair; *ic*, inner cortex; *m*, medulla; *ms*, meristoderm; *ms*, median segment; *p*, pit; *s*, segment; *ss*, lateral segment. (D after Woodworth; the rest after Oltmanns.)

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times two) of the other faces; this last segment (*ms*) is often as big as the remainder of the apical cell (cf. fig. 126 B, D). In *Pelvetia* and *Ascophyllum* the segmentation is stated to be less regular (see however (155) p. 423). The basal segments divide to form cells of the medulla, while the others divide into inner and outer cells as before.

Dichotomous branching generally takes place in *Fucus* soon after flattening has become apparent. It is initiated by a segment (usually representing half the initial cell) from one of the lateral faces assuming the form and functions of an apical cell. According to Oltmanns the two apicals thus constituted cut off a considerable number of large segments (fig. 126 E), which for a time undergo little division so that the initials are at first difficult to distinguish, although later they stand out clearly. Each apical cell then proceeds to form one limb of the dichotomy, while the intervening segments produce a mound of tissue which divides the apical slit into two. The dichotomous branching of *Pelvetia* and *Ascophyllum* takes place in the same way.

The abundant monopodial branching of *Ascophyllum* (cf. p. 327) is initiated close to the apex.[1] Longitudinal sections through the apical slit parallel to the surface of the thallus (fig. 127 D) disclose, on either side of the main apical cell (*a*), a number of initials (*1*, *2*) distinguished by denser cytoplasmic contents (cf. also fig. 127 A, *1*, *2*); they are derived from segments of the apical cell which have already undergone some further subdivision. Each such initial becomes sunk within a depression and, as further segments are cut off from the main apical cell, the initial is gradually carried over the margin of the apical slit on to one of the edges of the thallus (fig. 127 D, *3*, *4*). Here the depression assumes the form of a narrow slit drawn out parallel to the long axis of the thallus; in longitudinal sections it is often distinctly saccate at the base (fig. 127 D, *5*, *6*; E, *sl*). Meanwhile, as the marginal slit lengthens, the initials multiply (fig. 127 E, *1–3*; F, *si*), and it commonly becomes divided into several bays, with an apical cell at the bottom of each. At the base of the germling the primary lateral initial often grows out into a branch without forming others (fig. 127 C, *bs*), but on the more mature parts twelve or more initials may arise within a single slit. At first only one of these grows out, but others soon follow suit giving the familiar tufts of branchlets (fig. 115 D, F). The presence of numerous apical cells within the marginal slits admits of almost unlimited regeneration of laterals.

Seirococcus ((74) p. 12) shows similar features (fig. 127 A, B). The slit harbouring the four-sided apical cell (*a*) lies at the base of a rounded depression, covered in by the rudiments of the leafy laterals (fig. 115 A, *g*). The segments of the apical cell (fig. 127 A, *l1*, *l2*), situated between the initials (*1*, *2*), here divide to form mounds (*l3*) from which the leafy laterals (cf. fig. 115 A, *l*; G, *d–f*) are produced. As in *Asco-*

[1] I have followed the later account of Oltmanns ((179) p. 194), which does not altogether agree with the earlier one (178).

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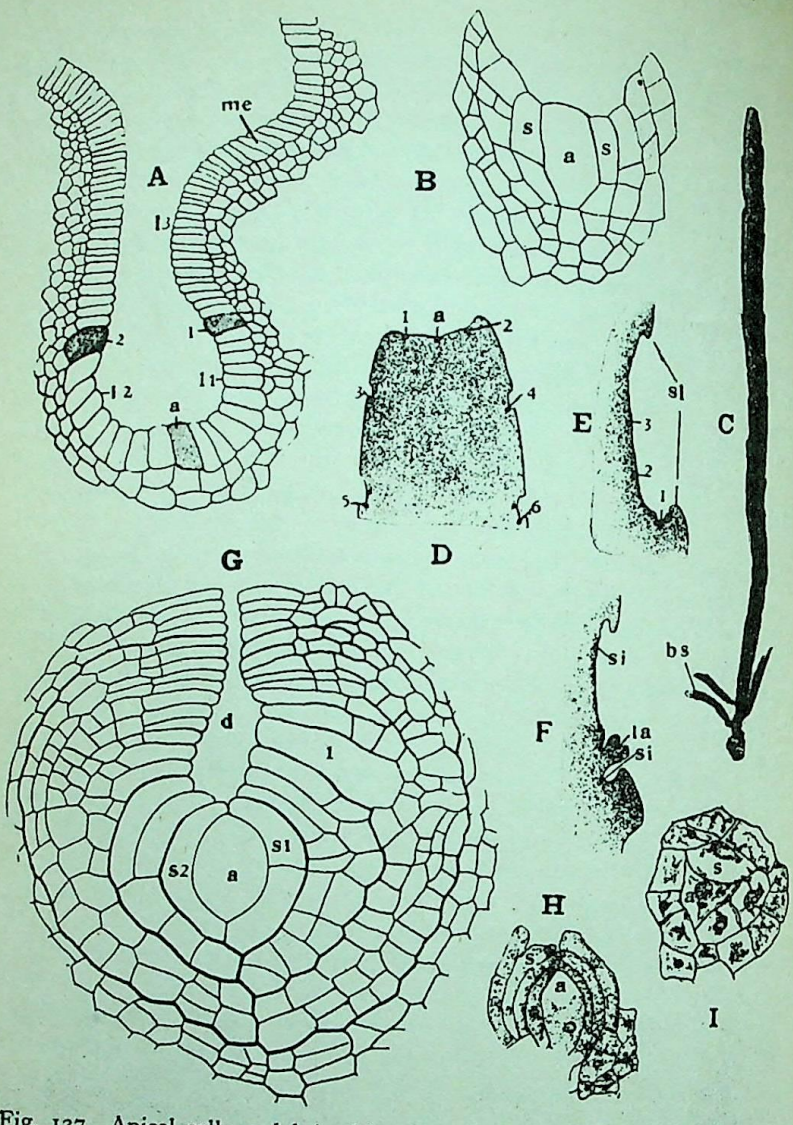

Fig. 127. Apical cells and branching in other Fucales. A, B, *Seirococcus axillaris* (Kütz.) Grev.; A, longitudinal section of apical depression, *1*, *2* apical cells of laterals, l_1, l_2, l_3 successive lateral lobes; B, vertical section through apical cell and adjacent segments. C–F, *Ascophyllum nodosum* (L.) Le Jol.; C, young plant; D, diagrammatic longitudinal section of apex in plane of flattening, *1–6* successive lateral initials; E, F, two of the marginal slits in longitudinal section, in F with an outgrowing lateral (*la*), *1–3* in E successive secondary initials. G, *Halidrys siliquosa* (L.) Lyngb., longitudinal section of apical depression. H, I, *Bifurcaria tuberculata* Stackh., apical cell in longitudinal (H) and transverse (I) sections. *a*, apical cell; *bs*, basal frond; *d*, apical depression; *l*, *la*, laterals; *me*, meristoderm; *s*, segment; *si*, secondary initial; *sl*, lateral slit. (A, B after Gruber; H, I after Rees; the rest after Oltmanns.)

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phyllum, the initials situated in the intervening bays increase in number and in part come to occupy the adaxial edge of the lateral; these secondary initials lie in depressions separated by small mounds which are clearly equivalent to the leafy laterals. Only few of these initials develop into branches of unlimited growth (fig. 115 A, *la*); most give rise to the fertile branches (*r*) which are of different ages.

The leaf-like laterals, which constitute the chief difference between *Seirococcus* and *Ascophyllum*, are in the latter represented by the inconspicuous mounds separating the initials (cf. fig. 127 A and D); were these to grow out in the same way, the resemblance to *Seirococcus* would be very marked. In the latter, neither the leafy laterals, nor the small outgrowths between the fertile branches, possess an apical cell.

The change from the three- to the four-sided apical cell in Fucaceae is evidently associated with the prevalent flattening and bilateral symmetry. In Cystoseiraceae and Sargassaceae, with a marked tendency towards radial organisation, the three-sided cell[1] of the germling persists throughout life. In most of them the apical depression is a deep funnel (fig. 128 A) filled with mucilage, but in *Halidrys siliquosa* ((74) p. 21, (178) p. 46, (197) p. 356) it takes the form of a deep slit, perpendicular to the plane of flattening (figs. 118 E; 127 G, *d*), and this is also essentially so in *Himanthalia* ((178) p. 68).

The lateral initials are produced in the same way as in *Ascophyllum*. In *Halidrys* (fig. 118 E, *1–4*) they arise alternately and with some regularity from certain segments (fig. 127 G, *l*), which undergo little division until the definitive three-sided apical cell is cut out within them by oblique walls. When the initials have passed out of the apical pit, each becomes lodged in a separate depression (fig. 118 E, *2*, *3*) and gives rise (*4*) either to a long or a short branch; when the latter has completed its growth, the initial divides into a group of cells and the apical depression disappears. Except for the differences in the early development (p. 338), matters are much the same in *Cystoseira* ((74) p. 52, (161), (197) p. 358, (280) p. 6), once the apical cell of the axis is established; in the radially branched species, however, the laterals are laid down on a 2/5 spiral (fig. 128 A).

The formation of the lateral branch-systems of *Sargassum* commences in the usual way (fig. 128 B). In *S. linifolium* ((178) p. 55) the apical depression becomes drawn out in the direction of the future branch and, when several branches arise at about the same level, it may appear star-shaped when seen from above. Soon after the initial has passed out of the apical pit, it cuts off a secondary initial (fig. 128 B, *b2*) on its distal side; the depression harbouring the two initials assumes the form of a radial slit, and they become separated by an intervening mound of tissue (*d*). After a short time the distal initial

[1] Apart from the instances referred to below, such a cell has been recorded in *Bifurcaria* ((191) p. 105), *Bifurcariopsis* ((305) p. 147), *Turbinaria* ((15) p. 224), and *Carpophyllum* ((41) p. 286, (45) p. 133).

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divides more rapidly than the other and develops into the subtending "leaf" (fig. 128 C, D, *b2*), whilst the proximal one (*b1*) comes to lie more or less definitely in its axil. The "leaf" (*b2*) is clearly a lateral which has pushed aside the parent axis (*b1*). The apical cell of the latter soon produces further initials, which are arranged on a 2/5 spiral and give rise to the other branches of the system, although the "leaf" does not form part of this spiral, in this respect behaving like a prophyll. It would be well if the development of the lateral branch-systems were studied in other species of *Sargassum*.

The segments of the three-sided apical cell of *Himanthalia* ((178), (210) p. 14, (275) p. 49) divide to form the tissue of the cup, whilst the

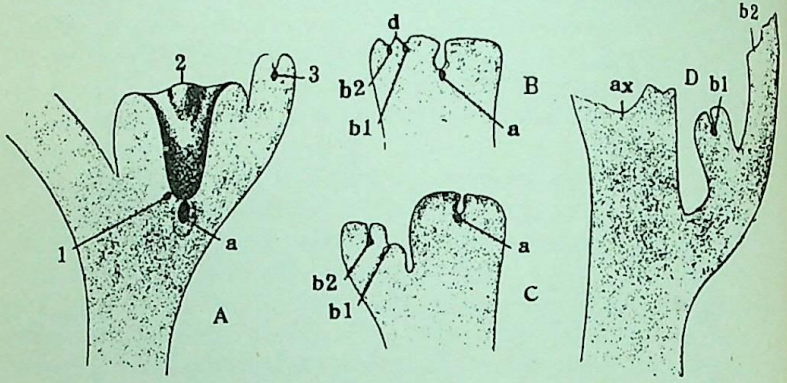

Fig. 128. Apical cell and branching of *Cystoseira* and *Sargassum*. A, *Cystoseira* sp., diagram of apex of a branching shoot, 1–3 successive initials. B–D, *Sargassum linifolium* (Turn.) Ag., diagrammatic longitudinal sections showing successive stages in branch-development. *a*, apical cell of axis; *ax*, axis; *b1*, primary and *b2*, secondary initial; *d*, the mound of tissue intervening between *b1* and *b2*. (A after Valiante; B–D after Oltmanns.)

receptacles represent one branch of a dichotomy. The cup can perhaps be compared to the main axes of a *Cystoseira* and the receptacles to the successively formed laterals.

The four (rarely three) apical cells, characteristic of *Hormosira* ((74) p. 4), are readily recognisable in a transverse section through the apex (fig. 129 B, *1–4*). They are separated by four thicker walls which are approximately perpendicular to one another and can be traced both in the peripheral direction and backwards into the substance of the thallus, where they terminate in the four bays of the central hollow (p. 344). The apicals are situated at the base of a shallow groove (fig. 129 A, *a*). Preparatory to branching the number of apical cells is increased by longitudinal division (fig. 129 G). In *Notheia* ((17) p. 419, (74) p. 7) transverse sections of the apex (fig. 129 D) show three apical cells which project slightly (fig. 129 E); for the details of

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branching see p. 365. Little is known of the early development of these two genera.

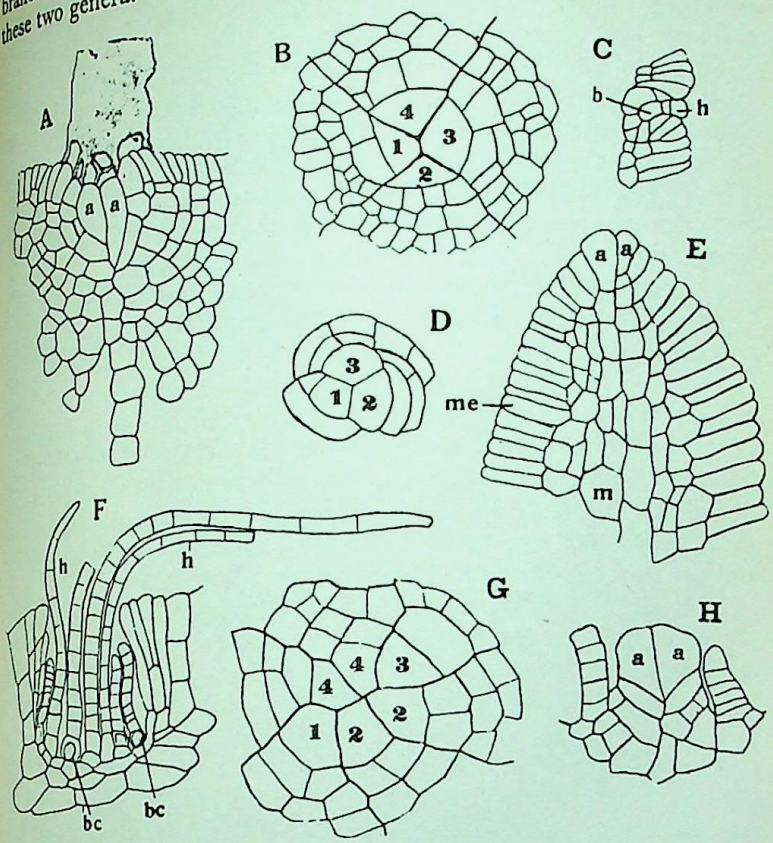

Fig. 129. Hormosiraceae. A, B, G, *Hormosira Banksii* (Turn.) Decsne; A, longitudinal and B, G, transverse sections of apex, *1–4* in B the apical cells; G shows multiplication of initials preparatory to branching. C–F, H, *Notheia anomala* Bail. & Harv.; C, early development of conceptacle in section; D, surface-view of apex, *1–3* the apical cells; E, longitudinal section of apex; F, section of young conceptacle with hairs; H, early stage in branch-formation. *a*, apical cell; *b*, basal cell of conceptacle; *bc*, basal cell of hair; *h*, hair; *m*, medulla; *me*, meristoderm. (After Gruber.)

ANATOMICAL STRUCTURE

Although the anatomy of the mature thallus has been examined in a considerable number of Fucales,[1] certain details still remain obscure. Investigation of fresh material and of material fixed and stained by new methods would probably shed light on obscure points. There are appreciable resemblances to the Laminariales, although the Fucales

[1] See (15) p. 221, (17) p. 419, (48) p. 10, (77), (85), (88), (89) p. 25, (178), (196), (197), (198) p. 96, (279), (288), (291), (305) p. 147, (306) p. 54.

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have not attained to the degree of anatomical specialisation that is evident in some of the former. The cells normally contain but a single nucleus which shows some differences in structure in the different families (211, 279).

As in Laminariales, the thallus is built up from two sources, viz. by the primary meristem (here usually an apical cell) and by the activity of the surface-layer of cells (meristoderm). The more definite character of the former renders the elucidation of its rôle in the formation of the thallus easier than in Laminariales. As shown in the previous pages, the first medullary elements arise from the inner cells of the embryo (fig. 125 E, *m*) before the establishment of an apical cell. Subsequently the medulla is increased by contributions from the inner halves of the segments of the latter (fig. 126 A, C; also from the basal segments in the Fucaceae, cf. fig. 126 B), while the outer halves of these segments add progressively to the meristoderm (*me*). The early separation (fig. 125 F) of the medullary cells (*m*), as a result of gelatinisation of the middle lamellae ((197) p. 327) of the longitudinal walls, is even more marked in the elements contributed from the apical cell (fig. 126 A, C, *m*). Here and there, however, the walls remain thin and constitute pits (*p*). Little mucilage appears to be formed in the medulla in Cystoseiraceae ((279) p. 42).

Soon after the differentiation of the apical cell, the inner parts of its segments divide a number of times without gelatinisation of the walls, and thus there arises a cortex (fig. 130 B, *c*) of relatively large, but closely arranged cells ((155) p. 425, (178) p. 19). Many authorities((77) p. 324, (197) p. 325, (291) pp. 503, 529) report tangential division of the surface-layer of cells with resulting additions to the cortex, and the gradual transformation of the innermost cells of the latter into medullary elements, but the degree of importance of these processes as compared with the contribution from the apical meristem is not clear. In the stipe of *Durvillea* there is evidently active division of the meristoderm ((87) p. 558). The general resemblance to the mode of origin of the different tissues of a *Laminaria* is obvious, and another point of similarity is that, despite the extensive gelatinisation of longitudinal walls, especially in the inner tissues, the transverse walls remain unaffected (fig. 130 C).

The cells of the peripheral layer at first multiply by anticlinal (often crosswise) division. This active surface growth, as in Laminariales, leads to passive stretching of the inner elements which, particularly in the flattened parts of the thalli, tend to be dragged out of their longitudinal course so that their arrangement often becomes very irregular (fig. 130 A, *m*), nowhere more evident than in the receptacles of *Fucus* (fig. 133 F), etc. Tissue-tensions, similar to those of Laminariales, are reported ((119) p. 841). In rapidly lengthening structures (e.g. the receptacles of *Himanthalia* (291)) the elongation of the medullary cells may be accompanied by frequent horizontal division.

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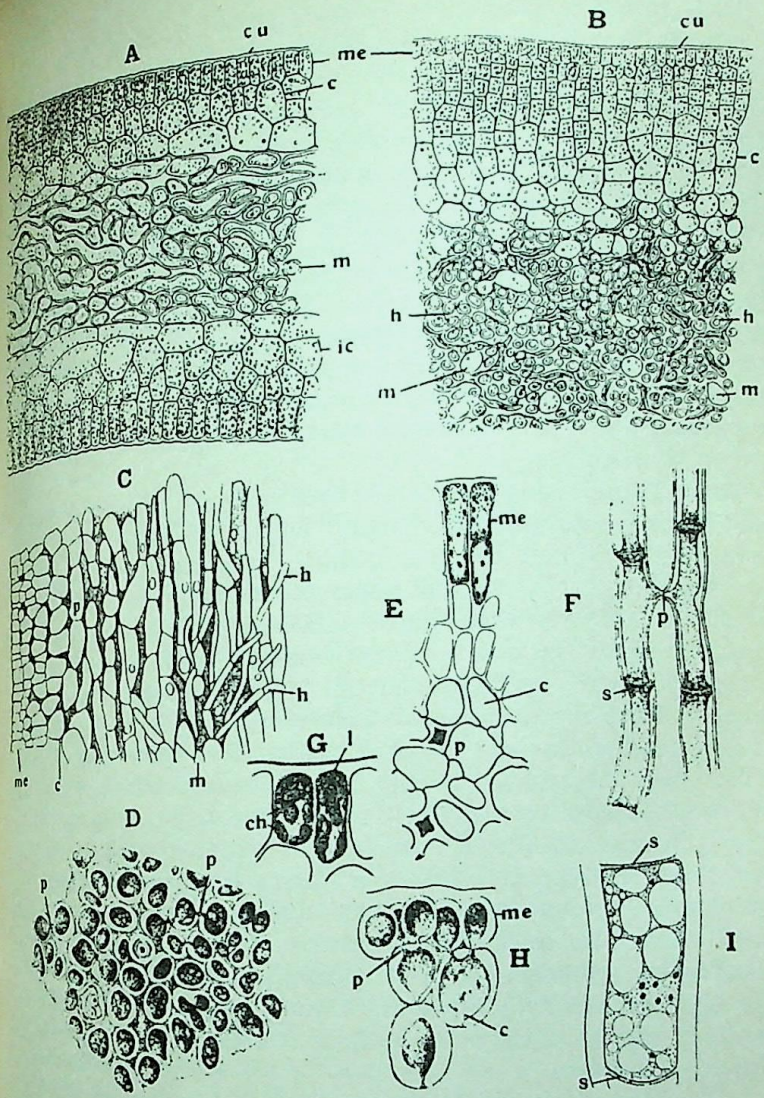

Fig. 130. Anatomy of Fucales. A, B, *Fucus* sp., transverse sections of A, wing and B, midrib of adult thallus. C, *Ascophyllum nodosum* (L.) Le Jol., longitudinal section, parallel to plane of flattening. D–F, *Pelvetia canaliculata* (L.) Decsne & Thur.; D, surface-view of thallus showing pits between the cells; E, transverse section of surface-layers of thallus; F, two medullary elements showing perforation of cross-walls. G, *Cystoseira ericoides* C. Ag., two surface cells in section. H, I, *Himanthalia lorea* (L.) Lyngb.; H, peripheral tissues in transverse section; I, cortical cell in longitudinal section showing perforated septa. *c*, cortex; *ch*, chromatophore; *cu*, cuticle; *h*, hyphae; *ic*, inner cortex; *l*, light-reflecting bodies; *m*, medulla; *me*, meristoderm; *p*, pit; *s*, perforated septum. (A–C after Oltmanns; D–F after Hansteen; G after Berthold; H, I after Wille.)

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The surface is covered by a mucilaginous "cuticle" ((85) p. 77, (178) p. 19, (191) p. 106; fig. 130 A, B, *cu*), which is sometimes thick and stratified, as at the apices of the fronds of *Halidrys*. The peripheral cells, especially in the younger parts, have a palisade-like shape (fig. 130 A, C, E, *me*), and the hypodermal layer may exhibit a similar form (291). The surface-cells are usually crowded with chromatophores (fig. 130 G) and abundant fucosan-vesicles, although according to Wille there are few chromatophores in the outermost layer of the mature receptacle of *Himanthalia* which he suggests acts as a light-screen. In surface-view the cells of the peripheral layer are usually separated by thin walls (cf. however (77) p. 321 and fig. 130 D), which sometimes show undulation ((77) p. 337, (191) p. 106, (275) pl. 24, fig. 2, (291) p. 506) although this may be an artefact. The cells are (always ?) connected with the internal elements by pits (fig. 130 H, *p*; (77) p. 324, (85) p. 78, (279) p. 41, (291)).

As in Laminariales, the cortical cells undergo little further division and gradually assume an elongate form (figs. 126 C; 130 C, *c*); towards the interior the longitudinal walls usually gelatinise ((77) p. 327, (291) p. 503) so that there is commonly an imperceptible gradation to the medulla. There is evidence of the formation of cross-connections (cf. fig. 130 F, *p*)[1] by extension of the pits left in these longitudinal walls ((46) p. 233, (77) p. 331, (88), (178) p. 17, (197) p. 330, (287)), but the special mode of formation of such connections, described for Laminariales (p. 227), has not been observed in Fucales. That cross-connections develop in some quantity is shown by the network of medullary elements found in the wings of the thallus of a *Fucus*, for instance. The cortical cells often contain much fucosan and have been regarded as fulfilling a storage function, while their frequent strong thickening indicates also a mechanical rôle; Henckel ((85) p. 78) regards the thickening as subserving water-storage in *Pelvetia canaliculata*. Simons ((245) p. 166) describes the central tissue of the axis of *Sargassum Filipendula* as consisting of narrow elongate cells, the inner with thin, the outer with thick walls; in the leaves only the former are present.

The extent of production of *hyphae* varies greatly in different Fucales. In *Bifurcaria* ((74) p. 23, (191) p. 108), *Pelvetia*, and *Notheia* ((17) p. 419) they are confined to the basal parts of the thallus, while a considerable number of the published figures of other genera afford no evidence of their presence.[2] Except near the attaching organs, they seem to be less prominently developed in Cystoseiraceae ((225) p. 145) and Sargassaceae

[1] Pennington's statement ((186) p. 268) as to branching and anastomosis of the medullary cells is probably due to misapprehension of this structural feature.

[2] Grabendörfer (72) reports no hyphae in *Durvillea*, but this is improbable and, judging by the figures of Herriott (87), they are abundantly developed, at least in the stipe.

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((77) p. 337, (245) p. 166) than in Fucaceae. As in Laminariales, the hyphae usually arise from the lower ends of the cells at the periphery of the medulla ((178) p. 17, (179) p. 210, (197) p. 332, (291) p. 502).

In *Fucus* the numerous hyphae of the midrib are produced only at a considerable distance behind the apex; as the midrib thickens, more and more develop so that, in sections of older parts (fig. 130 B), the original medullary cells (*m*) are embedded amid copious hyphae (*h*) which in the main run longitudinally. There are far fewer hyphae in the wings and these follow an irregular course, which adds to the confused picture presented by the medulla. These structures develop later in *Halidrys* ((178) p. 49) than in *Fucus*, but they become very abundant at the periphery of the medulla in the older parts. The *Ascophyllum*-thallus ((178) p. 41) possesses only scanty hyphae (fig. 130 C, *h*), although they are formed in considerable numbers near the slits from which the laterals emerge and also appear abundantly in the base of the lateral itself; these hyphae penetrate into the axis and intertwine with those of the latter, whereby a firm attachment is secured. The hyphae in the receptacle of *Himanthalia* run prevalently in a radial direction ((291) p. 517).

Although probably similar in origin, two kinds of hyphae have to be distinguished, viz. those with thin and those with strongly thickened walls; there are numerous transitions. Those of the former type, which may contain chromatophores ((291) p. 514) and possibly play a conducting rôle, are widely distributed in the flattened parts (fig. 130 C, *h*), while those of the latter type, which are no doubt essentially mechanical (Wille's "Verstärkungshyphen"), are to be met with in midribs (fig. 130 B, *h*) and other more or less cylindrical structures, especially in the older parts of the plant; they also occur in the narrow basal part of the receptacle of *Himanthalia* ((291) p. 515). Where such strengthening hyphae are lacking, the cells of the inner cortex evidently satisfy the mechanical requirements. The mechanical system may thus either be located towards the periphery or occupy a more or less central position, the latter arrangement evidently occurring in the main in the more permanent organs or in parts exposed to special strains (base of receptacle of *Himanthalia*).

Hypha-development is most marked in the neighbourhood of the *attaching discs*, which finally consist of a mass of branching and impenetrably interwoven hyphae ((77) p. 325, (178) p. 19, (197) p. 343). The discs of young plants (fig. 131 C) are formed partly by the outgrowth of peripheral cells and partly by the development, from the internal cells of the stalk of the embryo, of hyphae which penetrate to the outside. Further hyphae continually grow over the surface and extend the area of the disc, whilst increase in thickness is brought about by the production of new hyphae in the interior. The stalk of *Fucus* also gradually becomes overgrown with a layer of hyphae, but its marked thickness in older plants, as also that of the axes of *Cystoseira* for example, is only in part due to this superficial felt and

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to the internal production of hyphae. In the older regions there is marked *secondary meristematic activity* on the part of one or more layers of the cortex ((178) p. 22, (186) p. 270, (197) p. 334), the original surface-layer dying and being gradually shed. There is at present no information whether such secondary activity occurs also in other genera.

Sieve-like perforations traversed by cytoplasmic connections have been recorded in the pit-membranes, on the thin horizontal walls of the cortical and medullary cells (fig. 130 F), as well as on the septa of their cross-connections and of the conducting hyphae, by Wille ((287), (291) pp. 501, 505) and others ((15) p. 221, (49) p. 334, (77) pp. 328, 341, (85) p. 78). Other investigators have failed to find such perforations, although the contracted protoplasts commonly show a tendency to adhere to the pit-membranes ((191) p. 107). Callus is rarely reported ((46) p. 233, (305) p. 147). Certain workers ((49) p. 334, (88) p. 100, (155) p. 425) have described continuity of the cytoplasm through large openings in the walls of the medullary and cortical cells, but this requires verification. According to Hansteen ((77) p. 341) the medullary cells in *Sargassum* show scalariform thickenings on their walls.

The *air-bladders* originate not far from the apex as a result of surface growth, accompanied by increase in thickness of the cortex; this leads to rupture of the medulla, remnants of which are commonly found around the edge of the central hollow ((34), (48) p. 12, (106) p. 93, (179) p. 212, (197) p. 335, (204) p. 137, (280) p. 9). In *Fucus vesiculosus* and *Ascophyllum* (289) the inner surface of the bladder is occupied by a felt of short unbranched threads containing chromatophores, while in *Cystoseira* the cavity is traversed by one or more longitudinal strands of medullary tissue. In *Cystoseira* and in other Fucales the walls of the vesicles show varying degrees of tissue-tension ((119) p. 827), while they are stated ((38) p. 205) to be thicker in individuals of *Ascophyllum nodosum* growing in deeper water. The diaphragms in *Halidrys* ((179) p. 212, (289)) consist of isodiametric cells and are connected by longitudinal strands of fibre-like cells apposed to the wall of the bladder. Structures simulating air-bladders, found occasionally on the fronds of certain species of *Fucus*, have been studied by Richard ((204) p. 140).

It has been stated that there is no carbon dioxide within the bladders ((135), (137), (289) p. 9), but according to Colla ((34) p. 183) they contain the same gases as the atmosphere, carbon dioxide being at a maximum and oxygen at a minimum during the night. Those of *Ascophyllum nodosum* are stated to contain a higher proportion of oxygen ((38) p. 201), the amount varying seasonally, as well as from day to day. Wille (cf. also (290) p. 534) and Colla believe that the bladders have a respiratory significance and that the oxygen is that formed in photosynthesis, while others see in them merely a mechanism for decreasing specific gravity ((106) p. 88, (107) p. 33, (204) p. 143).

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WOUND-HEALING AND ADVENTITIOUS SHOOTS

The surfaces exposed as a result of the wearing away of the wings of *Fucus* become covered with a secondary cortex, the formation of which commences at the edge of the wound. On the other hand, when the inner tissues are laid bare by the breaking off or devouring of part of a branch, as happens especially in the Fucales of the littoral zone, the exposed medullary cells alone participate in the healing of the wound. The outermost divide actively by radial and tangential longitudinal walls (fig. 131 A) to produce a new layer that in certain respects recalls the callus of higher plants ((120) p. 154, (148) p. 15, (178) p. 73, (276) p. 576, (280)). At first this layer of dividing medullary cells

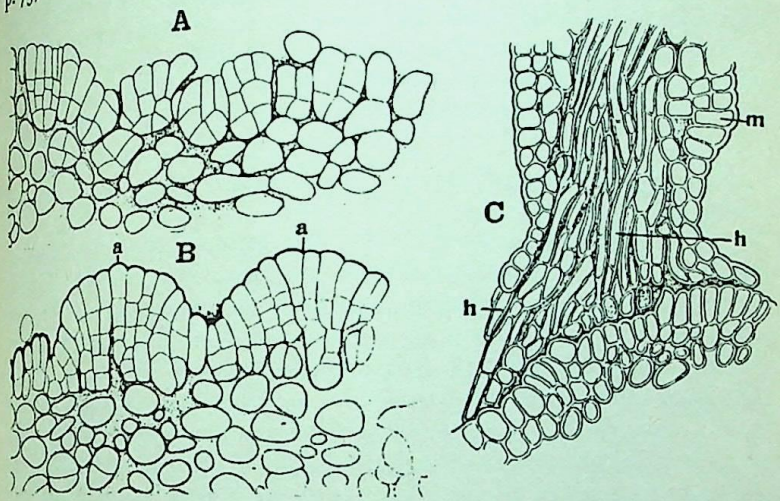

Fig. 131. *Pelvetia canaliculata* (L.) Decsne & Thur. (after Oltmanns). A, early stage in healing of a wounded surface in section; B, later stage of same, formation of adventitious growths (*a*); C, longitudinal section through base of a young plant. *h*, hypha; *m*, meristoderm.

is discontinuous, consisting of small mounds separated by undivided cells (fig. 131 A), and in *Pelvetia* ((178) p. 74) complete closure never seems to result. In *Fucus vesiculosus*, however, medullary cells below the wound also become active and, pushing between the surface-cells, divide like the latter so that the surface becomes completely covered. Wounding is nearly always followed by the formation of *adventitious branches* (cf. also (89) p. 24) which are often produced in some numbers from the small mounds formed by the medullary cells (fig. 131 B, *a*), a phenomenon which is particularly conspicuous in *Fucus vesiculosus* and *Pelvetia canaliculata*.

In *F. vesiculosus* (cf. also (197) pp. 322, 340, (228) p. 36) the formation of adventitious growths is mostly confined to regions containing hyphae

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(basal disc, stalk, midrib), although, except in the basal disc, these do not actively co-operate in their development. The shoots arising from the basal disc are formed by division of internal hyphal cells distinguished by denser cytoplasm, and the product breaks through the overlying tissue so that the development is endogenous. Numerous adventitious shoots commonly originate on the stalk from the regions where the wings have worn away. These diverse growths altogether resemble the young germlings, but few show any considerable development. They are not so common in *F. serratus*, but are frequently seen in *Pelvetia*, although here apparently not formed on the attaching organ. The adventitious shoots of *Cystoseira* (p. 338) have already been noticed. Herriott ((87) p. 562) records them on all parts of the stipe and frond of *Durvillea*, where they apparently develop endogenously.

Tobler (276) states that the bladders of *Ascophyllum* frequently contain Mytilidae (and Turbellarians) which enter as larvae through holes caused by Crustaceans. The interior of such bladders is lined by a compact cortex produced by division of the cells on the outside of the threads occupying the inner surface of the normal vesicle (cf. p. 360).

DEVELOPMENT OF THE CONCEPTACLES

The differentiation of conceptacles commences within the apical depression in the immediate vicinity of the apical cell, although they are carried out of the depression before development is complete. Bower (27) first showed that each conceptacle originates from a single initial cell; further details were elucidated by Oltmanns (178) and especially by Nienburg (163) to whom our present knowledge is largely due. Only a limited number of species have so far been studied. The considerable variations in the details of development fall into line with the classification of Fucales here adopted. Sterile and fertile conceptacles show the same early development ((245) p. 172).

The conceptacle nearly always originates from a superficial cell, which is distinguished by its larger size and a slower rate of division. In *Cystoseira* ((163) p. 3, (280) p. 11), *Sargassum* ((245) p. 169, (269), (316)) and *Carpophyllum* ((41) p. 289, (45) p. 133) the initial is flask-shaped and provided with a large nucleus (fig. 132 A). This divides unequally (fig. 132 B) and the products become separated by a markedly curved septum (fig. 132 C); the characteristically shaped upper cell (*t*) may with Simons be styled the *tongue-cell*. The lower cell (*basal cell*, *b*) then segments by two perpendicular walls (fig. 132 D). Meanwhile division of the surrounding cells leads to a gradual sinking of the products of the initial (fig. 132 E, F) and to separation of the tongue-cell (*t*) from the adjoining tissue. In *Sargassum* (fig. 132 G) and *Carpophyllum* the tongue-cell merely elongates or sometimes divides to form a row of a few cells ((41) p. 289, (245) p. 169), whilst in *Cystoseira* (fig. 132 F) it develops into a multicellular hair with a basal meristem. The inner lining of the conceptacle is almost entirely

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formed by vertical division of the lower cell (*b*) of the rudiment, which results in a gradual widening of the cavity; only the uppermost part is produced from the adjacent segments. Development of the conceptacles takes place in essentially the same way in *Halidrys* ((49), (163) p. 10, (178) p. 79).

In *Fucus* ((27) p. 38, (163) p. 7)[1] and its allies the initial (fig. 132 H, *i*) soon becomes lodged at the base of a deep and narrow cavity owing to rapid growth and division of the surrounding cells. The septum between tongue and basal cells is straight (fig. 132 I) and, after segmentation of the latter by vertical walls, the resulting cells divide transversely to form two layers (fig. 132 J, *b*); by this time the rudiment is already deeply sunk. The further division of the products of the basal cell provides only the tissue occupying the floor of the conceptacle, the greater part of the lining being derived from the adjacent cells. The tongue-cell commonly exhibits no further development and sooner or later collapses, but in *F. spiralis* ((27) p. 44) it sometimes divides to form a hair. Heine ((83) p. 565) records much the same series of events in *Xiphophora*.

A somewhat different development is found in *Pelvetia fastigiata*[2] ((155) p. 426, (163) p. 16), for here the initial first segments longitudinally (fig. 132 P) and this is followed by transverse division of the resulting cells. The two basal cells thus produced segment rather irregularly to form the floor of the conceptacle, although the greater part of the wall again arises from the adjacent cells (fig. 132 S); the two upper cells (*t*) develop into short hairs.[3] According to Nienburg the first division is not always vertical (cf. fig. 132 R), and this irregular segmentation is the rule in *Ascophyllum* ((163) p. 19, (178) p. 78) where, despite occasional vertical division, the initial usually gives rise to a mound of cells occupying the floor of the conceptacle; in other respects, however, the development is like that of other Fucaceae.

The rather scanty data indicate that, in Cystoseiraceae and Sargassaceae, a considerable part of the wall of the conceptacle is formed from the basal segment of the initial cell, whilst in Fucaceae this gives rise only to the floor. The characteristic tongue-cell, with its rather marked degree of persistence, is moreover found only in the former, i.e. in the forms with a three-sided apical cell. An intermediate type is furnished by *Bifurcaria* ((163) p. 16, (191) p. 110), where the tongue-cell soon collapses and a relatively large part of the conceptacle-wall

[1] Roe's (207) data on the development of the conceptacle of *Fucus* do not agree with any other observations and, until support from other sources is forthcoming, must be regarded as erroneous (cf. Nienburg, in *Zeitschr. Bot.* 9, p. 611 and (166) p. 184).

[2] According to Nienburg the statements of Holtz ((89) p. 33) on the development of conceptacles in this species are incorrect.

[3] A rather similar development is described by Barton ((15) p. 223) for *Turbinaria*.

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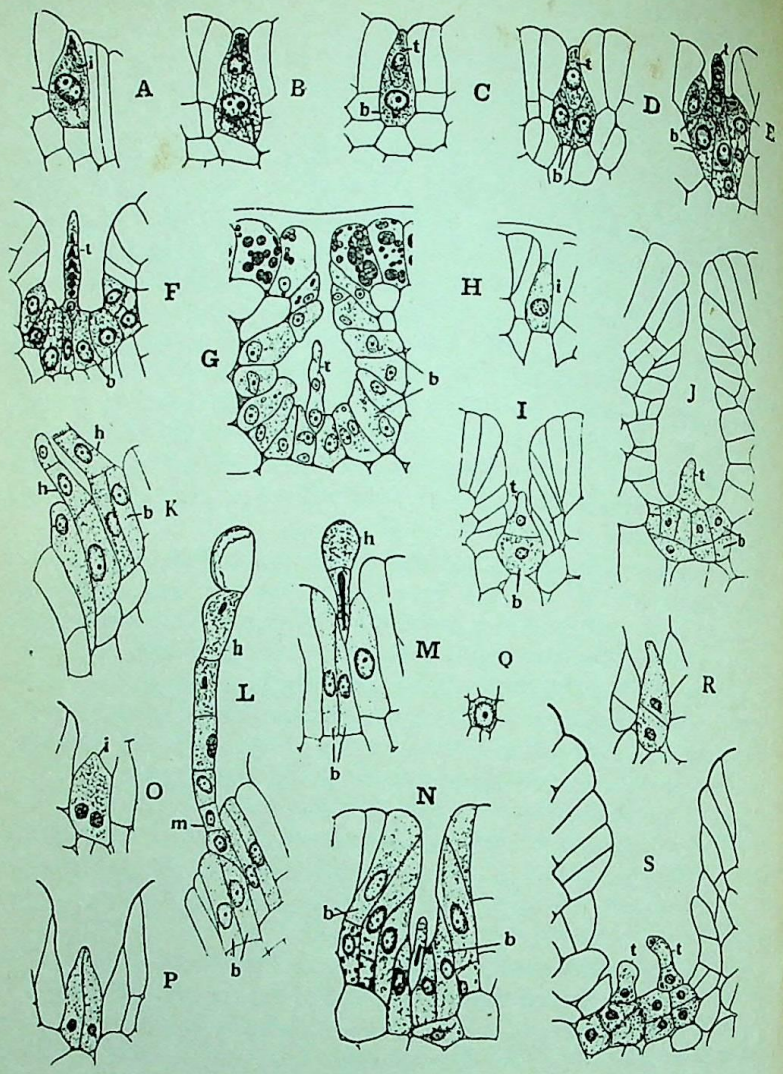

Fig. 132. Development of conceptacles. A–F, Q, *Cystoseira barbata* (Turn.) Ag.; A–F, sections of successive stages in formation of a conceptacle; Q, section of A in a plane at right angles. G, *Sargassum Filipendula* Ag., young conceptacle in section. H–J, *Fucus serratus* L., stages in formation of a conceptacle. K–N, *Himanthalia lorea* (L.) Lyngb.; K, section of apical depression of receptacle showing hair-formation; L, M, N, stages in conceptacle-development from basal cell of hair. O, P, R, S, *Pelvetia fastigiata* (J. Ag.) De Toni; O, P, S, successive stages in formation of a conceptacle; R, unusual early stage. *b*, basal cells and their products (shaded throughout); *h*, hair; *i*, conceptacle-initial; *m*, meristem; *t*, tongue-cell. (G after Simons; the rest after Nienburg.)

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is formed by the adjacent cells. In both respects there is resemblance to *Fucus serratus*.

In *Himanthalia* ((27) p. 45, (163) p. 12, (178) p. 80) the surface-cells within the depression at the summit of the receptacle soon grow out into hairs with a basal meristem (fig. 132 K, *h*). As this adds to the hair, the tip of the latter progressively disorganises (fig. 132 L, *h*) and, when the hair has been carried out of the depression, only the sunken basal cell (*b*) still persists. Certain of these basal cells function as conceptacular initials, dividing first by a vertical (fig. 132 K, L) and then by transverse walls. The central cells thus produced do not grow as actively as the marginal ones, which results in the formation of the cavity of the conceptacle, the entire lining of which arises from the products of the initial cell (fig. 132 N). The conceptacles of *Bifurcariopsis* ((305) p. 149) perhaps develop in much the same way.

The development of the conceptacle of *Himanthalia* shows that the tongue-cells of Cystoseiraceae and Sargassaceae, which are no doubt homologous with the upper cell of the rudiment in the Fucaceae, represent vestigial hairs which are suppressed to a varying degree. This means that the conceptacles take their origin to a more or less appreciable extent from the basal cell of a hair, and it is profitable in this connection to recall the perfectly similar derivation of the apical cell in the young embryo of *Fucus* (p. 349). The initial cells of the conceptacles may, in fact, be regarded as the equivalents of branch-initials which, like the latter, become lodged in a depression (the conceptacle), although diverted to a special purpose (cf. also (250) p. 778).

From this point of view the development of the conceptacle of *Notheia* ((17) p. 419; (74) p. 7) is of special interest. After transverse division of the initial (fig. 129 C) the upper cell develops into a hair (*h*), while the basal cell (*b*) gradually separates from the adjoining ones, its products apparently forming a large part of the lining of the conceptacle. As the latter enlarges, further hairs arise from the wall and form a projecting tuft (fig. 129 F). Later the upper parts of the hairs are shed, although their basal cells (*bc*), which have rich cytoplasmic contents, persist. There is some uncertainty as to the exact mode of development of the laterals (fig. 129 H, *a*) which arise from the conceptacles (fig. 124 E, *l*); Gruber believed that they were formed from the basal cells of the hairs (cf. however (17) p. 420). Several laterals may develop, although only one lengthens into a branch. A similar development of (adventitious) branches from cryptoblasts has been recorded in a salt-marsh form of *Fucus ceranoides* ((250) p. 775).

The association of reproductive organs with groups of hairs is frequent in the more specialised Phaeophyceae. In the Encoeliaceae (p. 109) these hairs commonly occupy the base of a depression, and it has been suggested ((179) p. 216) that this may show the mode of origin of the conceptacles of Fucales. The resemblance is, however, remote,

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and the little that is known as to the origin of these structures in Encoeliaceae implies an altogether different mode of development. In view of the probable absorptive functions of the hairs, their frequent association with reproductive organs requiring a localised food-supply may be but the outcome of a physiological need. On the other hand, the presence in young plants of many Brown Algae of an apical hair, at the base of which lies the meristem or at the base of which it subsequently develops (cf. (169) p. 60), shows that in Phaeophyceae a hair frequently precedes or is associated with meristematic activity, and this leads to the same conclusion as that arrived at above, viz. that the conceptacle is to be regarded as an arrested and specially modified branch or branch-system.

THE STRUCTURE OF THE MATURE CONCEPTACLES

All Fucales produce their sex organs within conceptacles and in many (*Pelvetia canaliculata*, *Ascophyllum*, *Halidrys*, *Bifurcaria*, *Himanthalia*) fertile conceptacles are alone present. In *Fucus*, *Sargassum*, *Turbinaria*, and others, cryptoblasts also occur scattered over the thallus. In *Sargassum Filipendula* ((245) p. 163) and various species of *Cystoseira* ((218), (225) p. 151) they even occur on the receptacles among the fertile conceptacles.

The lining of the conceptacles consists of a number of layers of flat cells (fig. 133 F, *w*), formed by tangential division of the primary cells and containing plentiful chromatophores. This wall separates the cavity from the loose medullary tissue. In the cryptoblasts the middle of the floor is occupied by an often extensive group of colourless unbranched hairs (fig. 133 A, *h*) with a basal meristem (*m*), similar to those found in other Phaeophyceae; they project in a tuft from the aperture, and in older cryptoblasts only the basal portions usually persist. Intermingled with them, and appearing in increasing numbers in later stages, are other shorter[1] pigmented hairs with diffuse growth; at first one-celled and more or less clavate (fig. 133 G, *p*), they later become multicellular and produce more or less numerous, usually unicellular branches. Their cells have dense granular contents and numerous small chromatophores. According to Nordhausen ((171) p. 291) they are largely responsible for producing the mucilage that fills the conceptacles.

The development of cryptoblasts is to some extent influenced by habitat conditions. They are specially abundant in those species of *Fucus* which are capable of withstanding prolonged drought and are particularly prominent in the salt-marsh forms of *F. vesiculosus*, where they tend to occupy a marginal position ((14) p. 367; fig. 138 C).

[1] These have been specially studied in species of *Fucus* (171), but are no doubt of wide distribution.

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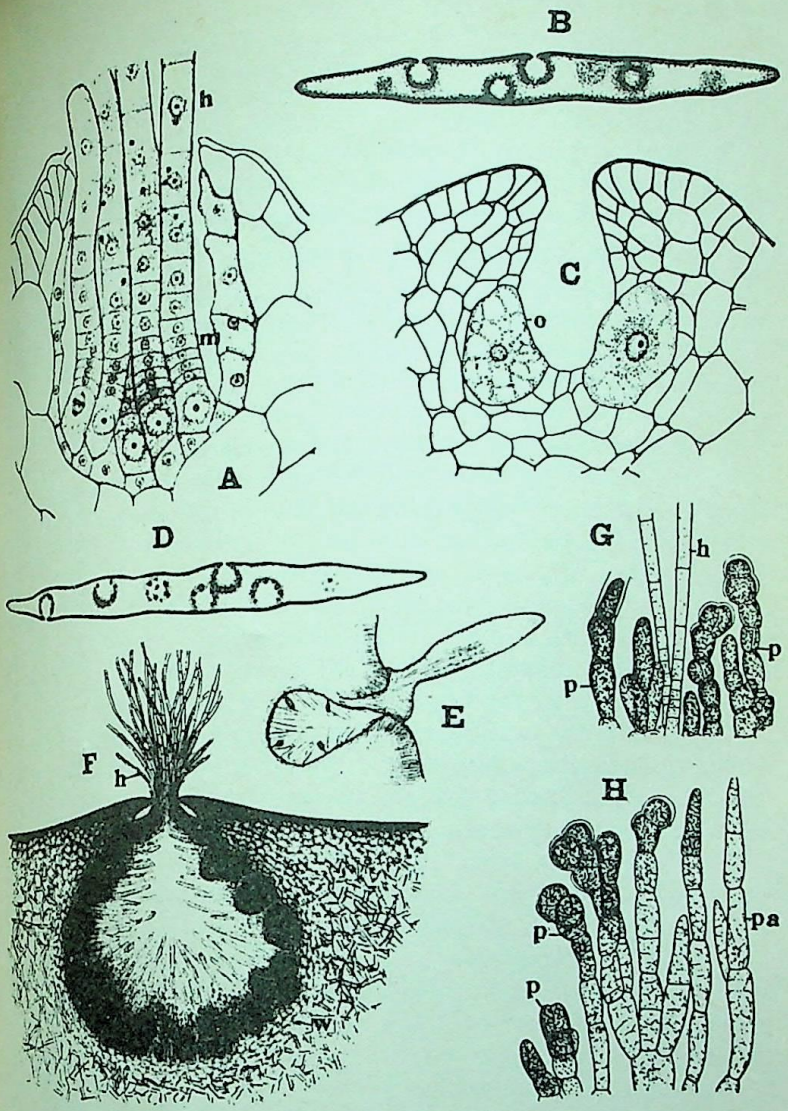

Fig. 133. Structure of conceptacles. A, *Sargassum Filipendula* Ag., section of a young cryptoblast. B, D, *Fucus serratus* L., sections of male and female receptacles respectively. C, *Sargassum linifolium* (Turn.) Ag., section of a young female conceptacle. E, *Notheia anomala* Bail. & Harv., young plant arising from conceptacle of *Hormosira*. F, *Fucus spiralis* L., section of a mature conceptacle. G, H, *F. vesiculosus* L., conceptacular hairs and paraphyses, G from a cryptoblast, H from a fertile conceptacle. *h*, hair; *m*, meristem; *o*, oogonium; *p*, *pa*, paraphyses; *w*, wall of conceptacle. (A after Simons; B, D, F after Thuret; C after Nienburg; E after Gruber; G, H after Nordhausen.)

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According to Gardner ((66) p. 9) *F. furcatus* is distinguished by having altogether closed cryptoblasts (caecostomata) devoid of hairs. The conceptacles of *Cystophyllum sisymbrioides* ((264) p. 6) are likewise without an aperture, the long hairs pushing their way through the superficial layer. In certain *Cystoseiras* (e.g. *C. Myrica*) the narrow cryptoblasts occur singly within small spinous branchlets, occupying their entire length ((218), (225) p. 152). Henckel (84) describes a *Cystoseira* lacking cryptoblasts and with hairs arising directly from the surface.

In the fertile conceptacles of *Fucus* ((171) p. 292), and probably also of other genera (cf. (155) p. 428, (291) p. 509), the colourless hairs are restricted to a small area near the aperture, from which they project markedly in *F. spiralis* (fig. 133 F, *h*). The greater part of the wall bears branched hairs (*paraphyses*, fig. 133 H, *pa*; cf. also (87) p. 558, (251) p. 34), in which the septa are often oblique and the component cells barrel-shaped with scanty chromatophores. In the male conceptacles these structures bear the antheridia (fig. 136 A) and are usually much more richly branched than in the female conceptacles, where indeed they sometimes remain unbranched (fig. 133 H). Between the paraphyses and the colourless hairs are others with abundant chromatophores, which correspond to the branched hairs of the cryptoblasts and exhibit transitions to the paraphyses (fig. 133 H, *p*). In *Himanthalia* ((291) p. 508) structures of the third type are not recorded. Only the hairs near the aperture take up stains readily.

The apparent identity in the early development of cryptoblasts and fertile conceptacles, quite apart from other similarities indicated by the above data, implies that the two are homologous. In *Sargassum* antheridia in various stages of abortion have been found in the cryptoblasts ((245) p. 173). The young conceptacles of *Notheia* possess the basal tuft of hairs characteristic of a cryptoblast (fig. 129 F), although these later disappear ((17) p. 420). In various species of *Cystoseira* (*C. abrotanifolia*, *C. foeniculacea*), also, long hairs resembling those of a cryptoblast occupy the centre of the fertile conceptacles ((218), (225) p. 151), the sex organs arising between them and the aperture. It may, therefore, be concluded that in forms possessing cryptoblasts the whole thallus once bore fertile conceptacles and that the present-day relegation of the latter to special receptacles is a secondary feature ((245) p. 174).[1] The Australasian *Myriodesma* ((6) p. 90), with a habit altogether like that of *Fucus* (cf. (82) pl. 24), in fact bears fertile conceptacles over the whole thallus.

SEXUAL REPRODUCTION

The distribution of sex organs varies considerably in different genera and even in one and the same species ((110) p. 189). Several are dioecious (many species of *Fucus* and *Sargassum*; *Ascophyllum*; *Himan-*

[1] Oltmanns ((178) p. 32), on the other hand, inclines to the belief that the fertile conceptacles are cryptoblasts which have become fertile.

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thalia; *Halidrys dioica*; *Coccophora* (252, 266); *Hormosira*; *Durvillea* ((87) p. 558), although the monoecious condition is perhaps the more usual. In many monoecious Fucales (*Pelvetia*, *Halidrys siliquosa*, *Bifurcaria tuberculata*, *Bifurcariopsis*, *Carpoglossum*, *Platylobium* (74)) the two sexes are found in the same conceptacle, but in others (species of *Sargassum*, *Phyllospora*, *Seirococcus*, *Scytothalia*) they occur in distinct conceptacles although on the same receptacle.

In the *Cystoseiras* above referred to, in which the conceptacles possess a basal tuft of hairs, the same receptacle harbours male, female, and hermaphrodite conceptacles ((225) p. 157). A similar condition occurs in some species of *Sargassum* ((75) p. 330), although many (e.g. *S. Horneri*) are dioecious. In this genus differences are sometimes apparent between the plants of the two sexes or more commonly between the two types of receptacles, the male being smooth, the female spinous, etc.; in *S. Horneri* ((117) p. 384) the male receptacles are longer and more slender. Differences between male and female plants are also recorded in *Halidrys dioica* (49). A few Fucales vary between monoecism and dioecism ((43) p. 250; see also p. 326).

In hermaphrodite conceptacles the oogonia and antheridial hairs are generally intermingled, but in *Bifurcaria tuberculata* and in many species of *Cystoseira* ((48) p. 14, (156) p. 129, (225) p. 156, (280) p. 12) the oogonia occupy the base and the antheridial hairs the sides of the conceptacles; in the former the oogonia develop later than the antheridia so that the young conceptacle appears to be male ((191) p. 109).

In *Cystoseira Montagnei* and *C. opuntioides* Sauvageau ((224), (225) p. 154) records two periods of fertility, conceptacles first appearing on the young branches and later, after these have grown to their full length, in terminal receptacles.

The oogonia ((178) p. 84, (275)) are nearly always borne directly on the wall of the conceptacle (fig. 133 D, F) and are usually provided with a definite stalk-cell which is either embedded in the wall (*Cystoseira*, (162) p. 168) or more usually stands above it (fig. 134 A, B, *s*); a stalk-cell is lacking in *Pelvetia canaliculata*. In *Sargassum* (fig. 133 C) and *Carpophyllum* the oogonia (*o*) are themselves to a large extent embedded ((117) p. 388, (162) p. 173). A different arrangement obtains in *Durvillea* (fig. 134 H, I), where the female organs are usually borne on branched hairs (286), although sometimes also arising directly from the wall ((87) p. 558). The occurrence on hairs is of interest, since it furnishes a parallel to the usual arrangement of the antheridia in Fucales.

The young oogonium, after the formation of the stalk-cell, is uninucleate, devoid of vacuoles (201), and commonly contains plentiful oil-drops ((19) p. 97). During its maturation there are probably always three successive nuclear divisions.[1] The first two (fig. 134 K) follow

[1] The contrary statement of Simons ((245) p. 176) for *Sargassum Filipendula* is corrected by Nienburg ((162) p. 168).

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rapidly upon one another and, at their conclusion, the four nuclei show a tetrahedral grouping; after this, there is normally a period of rest before the third division takes place ((53) p. 626, (255) p. 355). Strasburger, as well as Farmer and Williams, proved that reduction in chromosome-number occurs during the first nuclear divisions, while Yamanouchi (298) subsequently showed, both for the oogonium (fig. 137 E) and antheridium (fig. 136 O) of *Fucus*, that these divisions are meiotic; this has since been established also in diverse other genera ((95) p. 15, (116), (162), (172), (244), (267), (270)). Centrosomes (fig. 137 E, *c*) have usually been observed during the nuclear divisions in the oogonia and antheridia.

It is only in *Fucus* and *Notheia* ((17) p. 422, (150), (293) p. 638) that the cytoplasm undergoes cleavage into eight parts and that all the eight nuclei are used in the production of ova (fig. 134 B), which in *Fucus* exhibit some diversity in arrangement ((275) p. 30). In the remaining Fucales only some of the nuclei are employed in the organisation of ova, the supernumerary ones being extruded, sometimes together with a small quantity of cytoplasm. In *Ascophyllum* (fig. 134 O, P), *Xiphophora* (16, 306), *Bifurcariopsis* ((191) p. 113, (305) p. 152), *Hormosira* ((74) p. 3), and *Durvillea* there are four, in *Pelvetia* (fig. 134, L) two, and in all other Fucales only one functional ovum. It is clear, however, that the number of ova is not altogether rigid and diverse variants have been reported ((156) p. 141). In *Phyllospora* the single ovum is so large as to be visible to the naked eye ((293) p. 641).

In the mature oogonia of *Fucus* ((53) p. 628, (274) p. 201), *Xiphophora* (306) and *Hormosira* ((69) p. 270) the ova are separated by delicate septa (fig. 134 B), connected with the innermost layer of the oogonium-wall, although neither Oltmanns ((178) p. 84) nor Yamanouchi mention this feature. The presence of such septa would imply that the oogonium is plurilocular in nature. The two ova of *Pelvetia canaliculata* are separated by a thick gelatinous septum (fig. 134 L), although this is not so in *P. fastigiata*, where the ova show a collateral or oblique arrangement ((64) p. 130, (155) p. 428; cf. also (95) p. 12).

The production of four or eight ova is largely confined to the less specialised members of Fucales, and an oogonium producing eight female cells no doubt represents the primitive condition. It is of interest that the aberrant genera *Notheia* and *Hormosira* exhibit relatively primitive features in this respect. The supernumerary nuclei, representing aborted ova (fig. 134 J, L, O, *n*), sometimes show a considerable degree of persistence. In *Cystoseira* ((219), (225) p. 165) they may attract spermatozoids (fig. 134 M), and actual fusion between a spermatozoid and one of these nuclei has been observed, although the fate of the product could not be followed.

The unused nuclei take up diverse positions. In *Pelvetia* (fig. 134 L, *n*) they lie in the equatorial region between the two ova, while in *Ascophyllum* ((178) p. 86) they form a central group (fig. 134 O, *n*). Those

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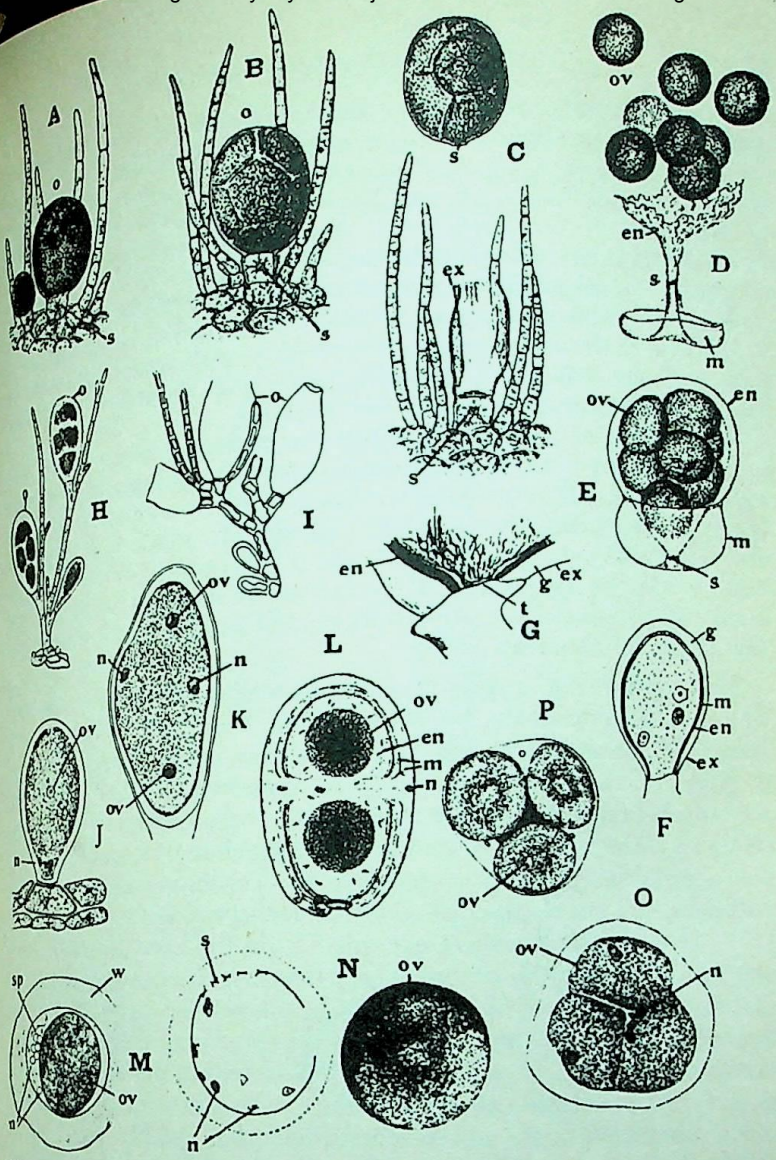

Fig. 134. Oogonia of Fucales. A–E, *Fucus vesiculosus* L.; A, B, stages in development; C, liberation of packet of ova; D, liberation of ova from same; E, earlier stage of the latter. F, G, *F. vesiculosus* L., structure of oogonial wall. H, *Durvillea potatorum* (Labill.) Kütz., oogonial hair. I, *D. antarctica* (Cham.) Hariot, the same, with dehisced oogonia. J, *Hesperophycus Harveyanus* (Decsne) Setch. & Gardn., mature oogonium. K, L, *Pelvetia canaliculata* (L.) Decsne & Thur.; K, young oogonium; L, the two ova with their envelopes. M, *Cystoseira foeniculacea* Grev., mature ovum with its envelope, at time of fertilisation. N, *Himanthalia lorea* (L.) Lyngb., extrusion of ovum. O, P, *Ascophyllum nodosum* (L.) Le Jol., mature oogonia. *en*, endochite; *ex*, exochite; *g*, mucilage; *m*, mesochite; *n*, extruded nuclei; *o*, oogonium; *ov*, ovum; *s*, stalk of oogonium; *sp*, spermatozoid; *t*, septum between stalk and oogonium; *w*, wall of oogonium. (A–E, L after Thuret; F, G after Farmer & Williams; H after Whitting; I after Skottsberg; J after Gardner; K, N–P after Oltmanns; M after Sauvageau.)

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of *Cystoseira* ((225) p. 163) float in the colourless liquid that occupies the space between the female cell and the oogonium-wall (fig. 134 M, *n*). In *Sargassum* ((2), (117) p. 391, (264) p. 8, (265) p. 144, (270), (304)) and apparently also in *Carpophyllum* ((41) p. 298) the ova contain eight peripheral nuclei at the time of discharge, seven undergoing disintegration during fertilisation; much the same is true of *Coccophora* ((267) p. 555). The single functional nucleus in *Hesperophycus* and *Pelvetiopsis* (64) undergoes considerable enlargement, while the remaining seven are cut off at the base of the oogonium, together with a small amount of cytoplasm (fig. 134 J, *n*), which is liberated together with the ovum; the further fate of this cytoplasmic mass is not known.

Application of pressure or subjection to higher temperatures may cause a number of the ova of *Fucus* to fuse; the resulting multinucleate eggs are apparently capable of fertilisation and sometimes develop into (polyploid ?) germlings ((39), (282) p. 300). By addition of potassium chloride to the sea-water, Tahara ((265) p. 145) caused persistence of all eight nuclei in *Sargassum*. If such ova are replaced in normal sea-water, all the nuclei are utilised in segmentation, though some of the germlings are abnormal.

The septum (fig. 134 G, *t*) between stalk and oogonium remains thin, but the rest of the wall of the latter thickens and becomes differentiated into several layers of which there are usually three ((53) p. 628). Of these (fig. 134 F, G) the innermost (endochite, *en*) and outermost (exochite, *ex*) are thin, whilst the intervening one (mesochite, *m*) is thick and separated from the exochite by a space (*g*). When the oogonium of *Fucus* is mature, the exochite ruptures and the contents, still enveloped by the two inner layers, are set free (fig. 134 C). The packets of ova are extruded from the aperture of the conceptacle in a quantity of mucilage; five layers are now stated to be distinguishable ((202); cf. also (306)). In the sea the inner part of the mesochite gelatinises and, as it swells, it ruptures apically and, slipping backwards (fig. 134 E, *m*), exposes the ova within the endochite ((274) p. 201); rapid solution of the latter and of the intervening septa leads to the liberation of the naked female cells (fig. 134 D). The ovum of *Himanthalia* ((70) p. 17) escapes through a small lateral rupture in the enveloping membranes (fig. 134 N).

In diverse Fucales the ova remain enclosed in part of the oogonial wall for a more or less prolonged period. A familiar example is furnished by *Pelvetia canaliculata* ((274) p. 208), where the two inner layers persist around the eggs until relatively late stages of embryo-development. The mesochite (fig. 134 L, *m*) is here very thick and mucilaginous ((275) p. 46), consisting of an outer structureless layer and an inner stratified one interrupted at the equator; in this region the mucilage seems to be specially soft so as to allow of the penetration of the sperms. The thick persistent envelopes are generally regarded as an adaptation to the extreme exposure to which this species of *Pelvetia* is subjected. Among the more specialised Fucales

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the liberated ovum often remains enclosed in the mucilaginous oogonial membranes, which form a kind of stalk adhering to the receptacle (fig. 135 A–C); the female cell is thus retained during fertilisation and the early stages of embryology.

In certain *Cystoseiras* the ova are liberated in a naked condition and are discharged successively and with considerable force from the con-

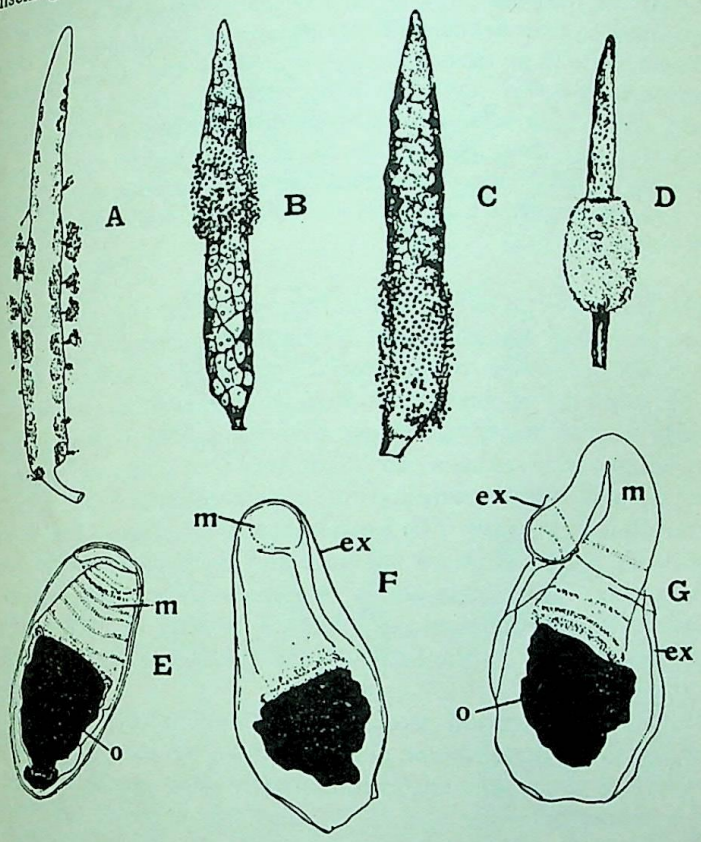

Fig. 135. A, E–G, *Bifurcaria brassiciformis* (Stackh.) Kütz. (after Delf); A, receptacle with extruded ova; E–G, stages in development of mucilaginous stalk of oogonium. B–D, *Sargassum Horneri* (Turn.) Ag., successive stages of extrusion of ova (after Tahara). *ex*, exochite; *m*, mesochite; *o*, ovum.

ceptacle ((225) p. 159); the receptacles commonly mature from below upwards. In others (e.g. *C. abrotanifolia*, *C. foeniculacea* (156) p. 135, (225) p. 161, (301) p. 319) the ova remain enclosed in the meso- and endochite and the former swells to form a long tube by means of which the ova are held on the outer surface of the receptacle. The same appears to occur in *Coccophora* ((266) p. 729). The oogonia of *Cystophyllum sisymbrioides*, and perhaps also of other species of the genus, are caught in the tangle formed by the projecting mucilaginous hairs of the conceptacle

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((264) p. 6). In several of the investigated species of *Sargassum* ((43), (116), (162) p. 174, (225) p. 167) and *Cystophyllum* (264), as well as in *Bifurcaria brassiciformis* (42,43), the extruded oogonia remain for some days firmly attached to the inside of the conceptacle by means of long gelatinous stalks (fig. 135 A–D) which, in *Sargassum Horneri* ((117) p. 390, (304)) and *Bifurcaria*, are formed by the thickened apex of the oogonial wall (of the mesochite ?, fig. 135 E, F). The lengthening distal end of the latter curves back (fig. 135 G) and becomes fixed to the inside of the conceptacle so that, as the stalk straightens, the oogonium is pushed out of the aperture in an inverted position. Much the same is reported for *Carpophyllum* ((45) p. 135). In *Marginariella* (44,47) the swelling mesochite forms a long tube, through which the contents of the oogonium pass before the three nuclear divisions occur and to the distal end of which the ovum remains attached. In *Bifurcariopsis* ((305) p. 152) the four ova are extruded separately on mucilage stalks formed from the mesochite.

The *antheridia* usually occur in large numbers (fig. 136 A, *a*) on the richly branched paraphyses of the male conceptacles (p. 368), very commonly occupying more especially the lower branches. A study of the development of these hairs, however, shows that the male organs actually occupy much the same position as the oogonia. The first antheridium arises from a cell of the wall ((27) p. 49, (298) p. 176), the resulting papilla later dividing into a stalk-cell (fig. 136 H, *st*) and the antheridium proper (*a*). The former usually produces a branch, which pushes the antheridium to one side and itself gives rise to a second antheridium. Since this series of events is generally repeated indefinitely, richly branched paraphyses like those of *Fucus* or *Pelvetia* result (fig. 136 A). In the final stages a number of sterile branches are produced.

Such richly branched structures are not, however, formed in all Fucales. Thus, in *Pelvetia fastigiata* ((89) p. 40, (155) p. 430) and *Notheia* ((17) p. 421) the antheridia usually arise directly from the wall of the conceptacle (fig. 136 H, I), and this is sometimes also so in *Cystoseira* ((156) p. 130, (301) p. 317), *Phyllospora* ((293) p. 641) and *Durvillea* ((87) p. 560); in *Turbinaria* ((15) p. 225), too, the hairs are stated rarely to bear more than two or three antheridia.

The antheridial initial of *Fucus* has a large nucleus with a prominent nucleolus (fig. 136 M), a number of yellow-green chromatophores, and alveolar cytoplasm ((76) p. 138, (122) p. 195). The first nuclear divisions (fig. 136 N, O), bringing about reduction ((1), (116), (298) p. 177), are succeeded by four further simultaneous mitoses, accompanied by multiplication of chromatophores which, however, no longer contain any pigment at the 8-nucleate stage (fig. 136 D). When 32 nuclei have been formed (fig. 136 E), the cytoplasm becomes divided ((122) p. 198, (155) p. 430, (206), (298) p. 179) by finely granular lamellae (*l*), similar to those observed in the maturing unilocular sporangia of Ectocarpales

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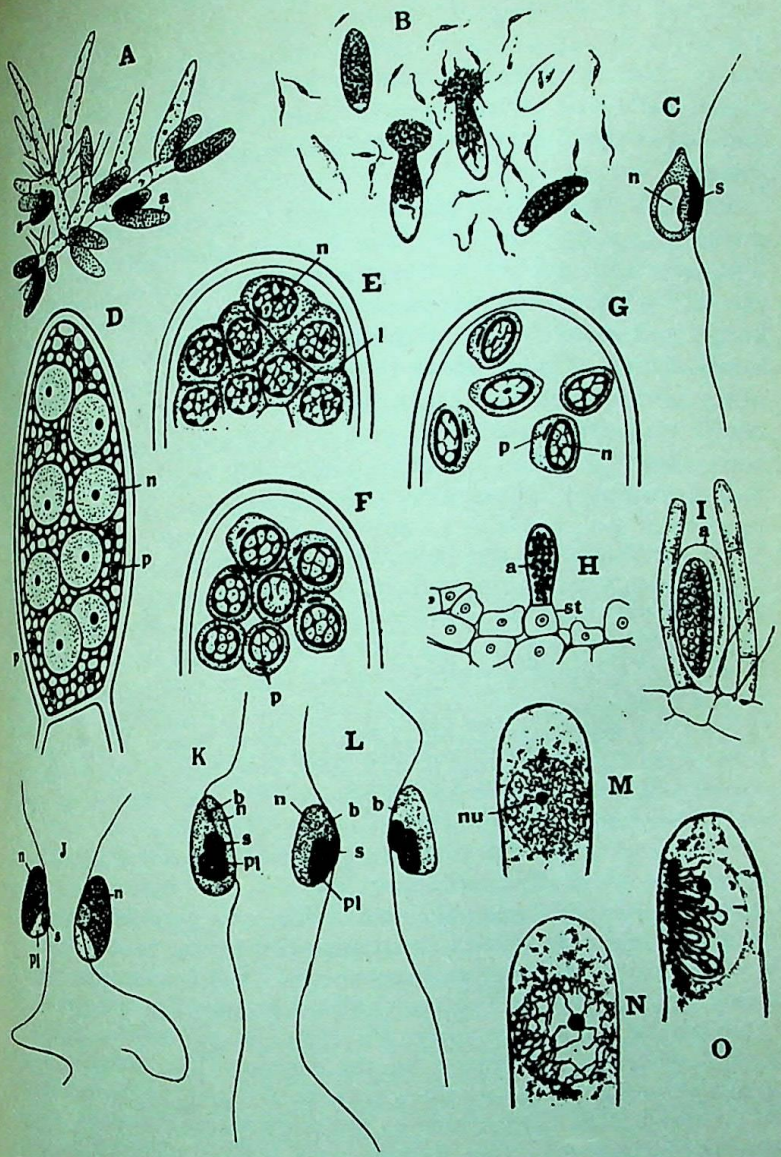

Fig. 136. Antheridia and antheridial development. A, B, *Fucus vesiculosus* L.; A, antheridial hair; B, liberation of spermatozoids. C, J, K, L, *F. spiralis* L., structure of spermatozoids, C an older figure, not altogether correct. D-G, *F. serratus* L., antheridial development; D, 8-nucleate stage; E, 32-nucleate stage, delimitation of cytoplasmic units; F, G, differentiation of spermatozoids. H, *Pelvetia fastigiata* (J. Ag.) De Toni, antheridium (*a*) on floor of conceptacle. I, *Notheia anomala* Bail. & Harv., antheridium. M–O, *Fucus vesiculosus* L.; M, young antheridium with resting nucleus; N, early and O, late stage of synezesis. *a*, antheridium; *b*, blepharoplast; *l*, cytoplasmic lamella; *n*, nucleus; *nu*, nucleolus; *p*, chromatophore; *pl*, plastomere; *s*, stigma; *st*, stalk-cell of antheridium. (A, B after Thuret; H after Moore; I after Barton; M–O after Yamanouchi; the rest after Kylin.)

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(p. 117). The last nuclear division results in the formation of 64 male cells (fig. 136 F; (19) p. 94, (274) p. 203). At this stage, according to Kylin ((122) p. 196), the somewhat enlarged chromatophores (*p*), of which there is ordinarily one to each nucleus, again develop an orange-yellow or yellow pigment, which is stated (206) to appear on one side of the plastid. Numerous fucosan-vesicles and oil-drops are present.

In the Fucaceae, and probably also in certain other Fucales ((76) p. 142, (275) p. 27), the wall of the mature antheridium is two-layered. The male cells, still enclosed in the inner layer, are extruded from the opening of the conceptacle as oblong packets embedded in mucilage. In the sea the enveloping membrane gelatinises at one (fig. 136 B), or rarely at both, ends to liberate the minute spermatozoids. Detachment of the entire antheridium takes place in *Halidrys*, *Cystoseira* ((48) p. 15, (225) p. 160), *Phyllospora* ((293) p. 641), and others, the spermatozoids being liberated within the conceptacle or in the sea; even when the former obtains, however, they probably pass out in a group.

The spermatozoids are generally pear-shaped, with the anterior end pointed and with the longer flagellum directed posteriorly (fig. 136 C). Their detailed structure has been much disputed. Behrens ((19) p. 95) and Strasburger ((255) p. 361) distinguished a large nucleus with a thin envelope of cytoplasm, while Guignard ((76) p. 142) concluded that the bulk of the body consisted of cytoplasm with a relatively small posterior nucleus (cf. also (122) and fig. 136 C). More recent investigations by Kylin and others ((125), (149) p. 278, (203), (206)) have, on the whole, supported Strasburger's view (cf. however (143), (144) p. 129) that the greater part of the body consists of nucleus (fig. 136 J–L, *n*).

The eye-spots (fig. 136 J–L, *s*) of the spermatozoids (cf. also (146)) are formed from the chromatophores (cf. however, (149) p. 289), which reacquire pigment during the final stages of antheridial development (cf. above); they are stated to contain only carotene, possibly with some xanthophyll. In *Pelvetia* and certain species of *Cystoseira* an eye-spot is lacking (220). Retzius ((203) p. 5) first observed other inclusions in the cytoplasm of the mature sperm (fig. 136 J–L, *pl*), which he suggested were mistaken by Guignard for the nucleus. They commonly occur singly, although sometimes there are several ((125) p. 75, (149) p. 280), and are believed to be comparable to the plastomeres frequently found in animal spermatozoa. The flagella arise from a blepharoplast (basal granule, fig. 136 K, L, *b*), which Meves regards as homologous with a centrosome. The longer posterior flagellum extends backwards within the body as far as the eye-spot, where it passes to the outside (fig. 136 J–L). According to Retzius ((203) p. 8) the flagella taper at their ends.

The mechanism of liberation of the sexual products is still not clear. Their escape can be observed if ripe receptacles are placed in a damp chamber. In the littoral Fucaceae mucilage, containing packets of ova and spermatozoids, is often seen at the apertures of the conceptacles

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during low water; in male plants these masses are commonly yellow in colour. With the advent of the next tide the gametes are freed and fertilisation can take place. It is tempting to suppose that in such forms the contraction of the thallus during low water plays some part in squeezing the packets out of the conceptacles, but this is in all probability not so ((53) p. 629). Extrusion frequently takes place during continuous submergence ((12) p. 61, (183), (228) p. 82) and Schreiber ((236) p. 280) observed the most marked liberation of sexual packets in *Fucus serratus* after the thallus had been under water. Oltmanns ((178) p. 93) states that it ceases after some time in drying plants, but recommences vigorously when they are returned to sea-water. Baker ((12) p. 56) concluded that the species growing at higher levels on the shore require a longer period of exposure for a maximum liberation of sexual products.

Oltmanns suggests that the most important factors causing liberation are increased turgor of the cells of the wall and the pressure of the mucilage within the conceptacle. This is in agreement with the fact ((238) p. 276) that more marked extrusion is observable in exposed plants after showers of rain, a phenomenon which can be reproduced artificially in the laboratory (cf. also ((121) p. 523). Increased turgor in the cells of the wall might result after inundation owing to concentration of the sap during exposure (cf. however (170) p. 36). In the many Fucales growing permanently submerged (*Cystoseira*, *Halidrys*, etc.) such external factors cannot come into play, although the rise and fall of the tide will involve alterations in light-intensity and in hydrostatic pressure that may affect turgor. Extrusion in *Cystoseira* has in fact been found to be accelerated by illumination ((184) p. 332) and in nature takes place during the early morning hours.

Among submerged Fucales a periodic liberation of the sexual products, not necessarily at regular intervals, has frequently been reported ((225), (263), (264), (265) p. 143, (267), (268)); Moser ((156) p. 132) records a regular fortnightly liberation in all the Fucales he examined. In such instances an intermittent production of mucilage within the conceptacle or periodic swelling of the mucilage is perhaps part of the liberation-mechanism. Escape of the sexual cells no doubt often follows the tidal rhythm, and this may remain so for some time during constant submergence ((70) p. 16).

As in other oogamous Phaeophyceae, fertilisation in Fucales takes place after liberation of the ova. If sexual packets from a ripe receptacle of *Fucus* are washed into a watch-glass, the liberation of the gametes and the process of sexual fusion are readily observed ((189) p. 144, (274), (306) p. 496), although fertilisation has been followed only in a few instances ((2), (52) p. 483, (255) p. 362, (277)). Large numbers of sperms (fig. 137 A) surround the ova, to which they become attached by the anterior flagellum, while the posterior one continues to move vigorously; in *Fucus* and *Ascophyllum* this is sufficient to set the egg in

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rotation. As soon as a spermatozoid has penetrated, the attraction ceases; Whitaker ((282) p. 298) describes the ensuing physical changes. During the rapid passage (fig. 137 C) of the minute male nucleus[1] (*m*) to the female (*f*), a centrosome (fig. 137 B, *c*) surrounded by faint radiations ((298) p. 184) becomes recognisable, whilst, after the male has penetrated the female nucleus, a second centrosome (*c'*) appears at the spot where the sperm (*m*) has entered. Occasionally several

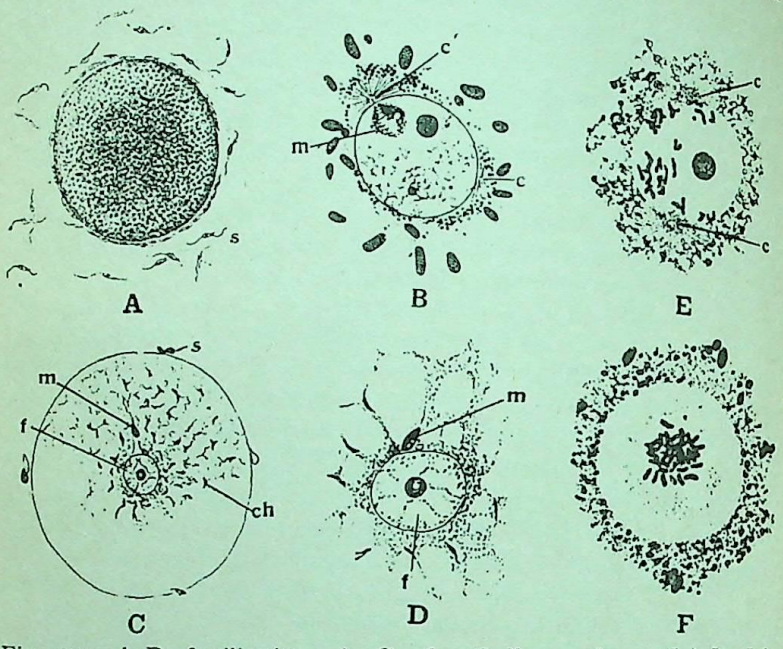

Fig. 137. A–D, fertilisation. A, C, *Ascophyllum nodosum* (L.) Le Jol.; A, spermatozoids and ovum; C, passage of male nucleus (*m*) to female (*f*). B, D, *Fucus vesiculosus* L.; B, penetration of male nucleus (*m*) into female; D, male nucleus (*m*) in contact with the female (*f*). E, F, *F. vesiculosus* L., nuclear division in oogonium; E, prophase of first division, 32 bivalent chromosomes; F, polar view of late prophase of third division. *c*, *c'*, centrosomes; *ch*, chromatophore; *f*, female and *m*, male nuclei; *s*, spermatozoid. (A after Thuret; C, D after Farmer & Williams; the rest after Yamanouchi.)

sperm-nuclei pass into the female nucleus and, when this is so, a corresponding number of centrosomes appears, which proves that the second centrosome observed in normal fertilisation is associated with the penetration of the sperm. This centrosome is possibly derived from the blepharoplast of the spermatozoid. During the first hours succeeding fertilisation there is a great increase in oxygen-consumption (283). Abe (2) failed to observe centrosomes in *Sargassum*.

[1] Behrens ((19) p. 102) no doubt interpreted binucleate ova as stages in fertilisation (cf. (52) p. 483).

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In *Halidrys* ((53) p. 634), at the time of fertilisation, the surface of the female cell is covered with conical projections bearing a number of fine threads, although these disappear after 3–5 minutes. Similar features have been recorded in *Cystoseira* ((104) p. 746, (156) p. 138) and in *Fucus*-eggs treated with hypotonic solutions (57). Winkler (296) observed penetration of spermatozoids into non-nucleated fragments of *Cystoseira*-eggs, some of which afforded germlings of small dimensions; Moser ((156) p. 173) failed to obtain their germination.

In view of the frequent dioecism fertilisation can only be achieved, if there is a simultaneous production of large numbers of gametes which become intermingled by water-movements; there must, however, be enormous wastage ((236) p. 285). The heavy ova tend to sink, although in the sublittoral Fucales the devices described on p. 373 keep the female cells *in situ*. According to Kotte (112) the spermatozoids of *Fucus serratus* are negatively phototactic and aerotactic, as well as positively geotactic, so that they will tend to follow the sinking ova. Chemotactic attraction is stated to be due to a substance excreted from the latter and the response is a phobic one (cf. also (105) p. 651). Bordet (26), however, maintains that the sperms are mainly sensitive to contact.

Parthenogenesis, which has been induced experimentally in *Fucus* ((181); cf. also (265)), has not been observed in nature ((110) p. 202) and germination of unfertilised eggs is only rarely recorded. In suggesting possible parthenogenesis in *Notheia*, Williams ((293) p. 639) does not refer to Barton's record of antheridia.

In view of the mixed populations of Fucales found on many shores, it is likely that hybridisation will occur, although there are few satisfactory records of the presence of hybrids in nature. When spermatozoids of one species are brought together with ova of another species of the same or of a different genus, there is active attraction, although fusion only ensues in certain instances. Thuret ((274) p. 206) first recorded fertilisation of the ova of *Fucus vesiculosus* by the spermatozoids of *F. serratus* and the putative hybrid has been described by Sauvageau ((215) p. 166, (217)). Thuret was, however, unsuccessful with other Fucaceae and failed to obtain the reciprocal cross between the species mentioned, although this was subsequently achieved by Kniep (109). Gard (62) describes a supposed hybrid between *F. spiralis* and *F. ceranoides*. Williams (292) obtained some positive results in crossing *Ascophyllum* with species of *Fucus* and records a plant intermediate between the two genera (cf. also (156) p. 152).

Kniep ((109) p. 333) achieved a large number of crosses between *F. spiralis* and *F. vesiculosus*, with either parent as the male. Ova of the former were obtained by incapacitating the sperms by brief immersion in a 1% solution of chloral hydrate in sea-water or in 10% alcohol; mature oogonia were also dissected out of the conceptacles. The sperms are readily separated from the rapidly sinking ova. Sauvageau ((215) p. 161) has described probable hybrids between the two species (fig. 114 E, p. 325); these resemble *F. vesiculosus* in the

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presence of bladders and in being dioecious, while the receptacles are more like those of *F. spiralis*. It still remains doubtful, whether these and other similar transitional types, found at the limits of the zones occupied by the various species of *Fucus*, are actual hybrids or habitat-forms. In commenting on this point, Kniep ((109) p. 337) suggests that the apparent scarcity of hybrids in nature may be due to unsuitability of the habitat or to inability to withstand competition with the parent-forms.

THE AFFINITIES OF FUCALES

Many authorities have assumed a certain measure of relationship between Laminariales and Fucales which have been regarded as lines diverging from a common ancestral source comprising forms like the Ectocarpales (cf. e.g. (110) p. 187, (124) p. 57). In both Laminariales and Fucales the thallus is a large diploid parenchymatous body which, despite differences in the method of growth, shows a considerable degree of similarity in anatomical structure, although displaying merely the culmination of tendencies manifest already among the polystichous Ectocarpales. Perhaps a fuller investigation of the Antarctic genera *Durvillea* and *Ascoseira* will shed light on the nature of this relationship. There are, however, very significant contrasts in reproduction between the two orders, since in Fucales a separate gametophytic phase is altogether lacking. The frequent reduction, in cultures, of the female gametophyte of Laminariales to a unicellular state, a condition which is apparently the rule in *Saccorhiza* (p. 251), has been regarded as illustrating a stage in the retrogression of the haploid phase which has culminated in the condition found in Fucales ((110) p. 185, (124) p. 57, (260) p. 184, (261) p. 372, (262) p. 44). The first two nuclear divisions in the oogonium are interpreted as a tetrad-division within a sporangium (cf. also (256) p. 4) in which, however, the spores are not individualised. Each, after a brief resting period, gives rise to two potential ova which represent all there is of the female gametophyte. It is not so easy to extend this interpretation to the antheridium.

It may be doubted, moreover, whether any such detailed attempts at homology are profitable, since there can be no question of any direct derivation of Fucales from Laminariales or other specialised group of Phaeophyceae. It seems more probable that the reproductive mechanism of the former has originated from the tendency for the asexual zoospores to behave as gametes, evident in diverse evolutionary lines among the less specialised Brown Algae (cf. pp. 128, 131, 187). Such a view does not necessitate the assumption of a reduced gametophyte, although, like the hypothesis stated above, it ultimately derives the sex organs of Fucales from unilocular sporangia. Kylin ((128) p. 439) suggests such a possibility, although sceptical as to the fusions

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between the swarmers of unilocular sporangia. Whether the occurrence of septation in the antheridium is a valid argument against such a hypothesis ((129) p. 310) can only be determined when the nature of this septation is better known. There can be no doubt that the Fucales have a long history behind them, and it is inadvisable to probe too deeply into homologies.

In recent years Kylin ((126) p. 77, (127) p. 28), laying stress on the differences in the relative lengths of the flagella of the spermatozoids of Fucales on the one hand, and of the zoospores of Phaeophyceae on the other, as well as on the probable plurilocular character of the antheridia, disputes the probability of a direct derivation of Fucales from forms resembling the present-day Ectocarpales. The evidence on the former point is conflicting ((46) p. 227, (145)), while, if the sex organs of certain Fucales acquire a plurilocular character at maturity, this appears to be secondary and altogether different from the condition shown by a typical plurilocular sporangium.

In the opinion of the writer (cf. also (312) p. 82) the Fucales have originated in the evolutionary line exemplified by the parenchymatous (polystichous) Ectocarpales, among which there is replacement of trichothallic by apical growth (p. 112), as apparently occurs also in the germling of *Fucus* (p. 349). As already emphasised, however, the derivation is remote and there appear to be no intermediate forms. The few, uncertain, fossil forms that have been ascribed to Fucales ((67), (185) p. 94) do not afford any clues. The suggested relationship with Encoeliaceae, already discussed on p. 365, does not carry one any further. Delf ((46) p. 236), in assuming an affinity with Mesogloeaceae, overlooks the fundamental differences in basic construction. The filamentous character of the medulla in the Fucales originates secondarily from a primary parenchymatous state, and there is no evidence whatsoever that the parenchymatous type of thallus in Phaeophyceae is derived from the pseudo-parenchymatous one, although Church ((33) p. 32) made such an unwarrantable assumption and Schussnig ((237) p. 265) evidently has some such hypothesis in mind.

Many of the less specialised members of the Fucales are characteristic of the colder seas of the Northern and Southern Hemispheres, whence they have invaded the warmer areas of the world. That such widespread genera as *Cystoseira*, *Cystophyllum*, and *Sargassum* are comparatively recent and still in course of vigorous evolution is shown not only by their morphological features and the presence of a single ovum in the oogonium, but also by the multiplicity of ill-defined species.

The following is an epitome of the classification adopted in the foregoing account (cf. (103) p. 179, (179) p. 186):

1. *Fucaceae:* Ascophyllum, Axillaria, Cystosphaera, Fucus, Marginariella, Myriodesma, Pelvetia, Pelvetiopsis, Phyllospora, Scaberia, Scytothalia, Seirococcus, Xiphophora.

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2. *Himanthaliaceae:* Himanthalia.
3. *Cystoseiraceae:* Bifurcaria (Pycnophycus), Bifurcariopsis, Carpoglossum, Cystophora (incl. Blossevillea), Cystophyllum, Cystoseira, Halidrys, Landsburgia, Platylobium, Platythalia.
4. *Sargassaceae:* Acystis, Carpophyllum, Coccophora, Sargassum (incl. Anthophycus, Pterocaulon), Turbinaria.
5. *Hormosiraceae:* Hormosira, Notheia.
6. *Durvilleaceae:* Durvillea (incl. Sarcophycus).
7. *Ascoseiraceae:* Ascoseira.

THE ECOLOGY OF FUCALES

Some reference has already been made to the marked zonation exhibited by the littoral Fucales on northern shores. *Pelvetia canaliculata* and *Fucus spiralis* occupy the uppermost, *F. serratus* and *Himanthalia* (fig. 117 A) the lower levels, with *Ascophyllum* and *Fucus vesiculosus* (fig. 117 B) in intermediate positions ((37) p. 23, (98) p. 64, (99) p. 191); on more northerly coasts ((22) p. 743, (101) p. 110, (209) p. 195) *F. inflatus* usually replaces *F. serratus*, while on the west coast of Sweden the place of *Pelvetia* is taken by *Fucus spiralis* ((121*a*) p. 225). On shores exposed to the full force of the waves *F. serratus*, *Ascophyllum* ((73) p. 418, (99*a*) p. 321) and *Himanthalia* ((101*a*) p. 8) are often lacking (cf. however (101) p. 112), while on wave-swept coasts in the Faeroes Boergesen found only *F. spiralis* and *F. inflatus*. Cotton records a bladderless variety of *F. vesiculosus* (var. *evesiculosus*) in such habitats and states that the size of the frond (cf. also (101) p. 30, (204) p. 140) and the number of bladders in the type increases with the degree of shelter. Rees ((194) p. 85; cf. also (303)) produces similar data for the distribution of littoral Fucales in relation to intensity of surf-action, although he points out that other factors concerned are the angle of slope and the nature of the surface of the rock (cf. also (101) p. 109, (192)). The relative levels of *Ascophyllum* and *Fucus vesiculosus* vary ((22) p. 744, (37) p. 55, (101) p. 111, (228) p. 63) and Zaneveld ((300) p. 447) discusses the possible causes. By contrast to the abundant representation of Fucales in the littoral region on northern shores, the bulk of the New Zealand members occur at and below low tide level ((176) p. 518), *Hormosira* being the chief emergent form.

There can be no doubt that the littoral Fucales are well adapted to their habitat. *Fucus vesiculosus*, *F. serratus*, and *Ascophyllum nodosum* are resistant to cold ((123), (168) p. 7, (253) p. 50), while in summer the thalli may reach a temperature of 34–36° C. without apparent harm, although Grubb ((73) p. 413) states that *F. serratus* is more susceptible to summer-heat than *F. vesiculosus*. The pronounced zonation is no doubt to a considerable extent a result of a differing capacity to resist desiccation ((11), (12), (35), (73) p. 421, (108) p. 123), both during germination and vegetative growth. According to Zaneveld ((300) p. 459) the forms in the upper zones have thicker membranes, a higher water-

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content, and reach their dry weight on evaporation later than those in the lower (cf. also (96), (188), (232) p. 536). Baker ((12) p. 67) also draws attention to the dilated receptacles filled with mucilage, characteristic of the species occupying the upper levels. *Halidrys siliquosa* by contrast cannot withstand even a short period of desiccation ((253) p. 50) and *Laminaria*, although more resistant (97), is very susceptible to frost. *Fucus evanescens* is likewise resistant to desiccation (158).

F. vesiculosus and *F. ceranoides* can withstand lowered salt-concentrations (31, 205), while the other two British species do so less readily (cf. also (105) p. 658). Such conditions have no effect on the formation of receptacles which are, however, sterile; cryptoblasts, on the other hand, are reduced in number or lacking. Kniep (105) was of the opinion that the increasing salt-concentration at lower levels played a rôle in the distribution of the littoral Fucales.

It is improbable that the practical restriction of the littoral Fucales to the intertidal region is dependent on illumination, although Gail (59) concludes that the lower limit of *Fucus evanescens* is determined by this factor. Montfort (153), however, investigating photosynthesis of *F. vesiculosus* at various depths, decided that the distribution of this species is not influenced by depth of submergence (cf. also (190a) p. 70). Both it and *F. serratus* ((51), (92) p. 134) are adapted to high light intensities and are the equivalents of sun-forms among land-plants. At the same time they can also carry on effective photosynthesis in relatively feeble light, and their active growth during the early months of the year is due to this capacity at a time when respiration is inconsiderable owing to the low temperature ((92) p. 134). There is evidence that in both species there is a seasonal variation in reaction to light and temperature (154). Stocker and Holdheide (253) found that considerable photosynthetic gain is possible even during periods of exposure, although the capacity for photosynthesis is gradually lost on drying; this is, however, accompanied by a reduction of respiration to a minimum. Exposure to rain results in a reduction of photosynthesis.

The littoral Fucales thus constitute a distinct ecological group, markedly adapted to a subaerial mode of life and with a great capacity to resist extreme conditions and to effect considerable assimilatory gains under such circumstances. Their adaptation to subaerial conditions is likewise displayed by the plentiful occurrence of forms of the diverse species concerned in the vegetation of salt-marshes.

Although the members of this order are normally lithophytes, they are also widely represented by unattached growth-forms which lack the attaching discs of the saxicolous types and for the most part propagate solely by vegetative means. Such forms are often a conspicuous feature of the flora of salt-marshes,[1] where they are found embedded in the mud or interlacing with one another and with the

[1] See especially (13), (14), (30), (37) p. 78, (194) p. 114.

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stems of the halophytic seed-plants so that they are not dislodged by the tides. They probably play an important rôle as pioneers, following upon the filamentous Green and Blue-green Algae that constitute the primary colonisers, and form a seed-bed (fig. 137 *bis*), as well as a protection during early stages of germination, for the phanerogamous halophytes ((13) p. 282, (14) p. 371). Most of them are of course subject to desiccation for a number of days in each fortnight, in place of the usual daily exposure. On the coasts of Morocco, near the southern limit of its range, *Fucus vesiculosus* is represented only by salt-marsh forms (147).

Most of the littoral Fucales, except *Himanthalia*, have given rise to such growth-forms on British salt-marshes. Apart from the prevalent vegetative reproduction, these forms are characterised by a

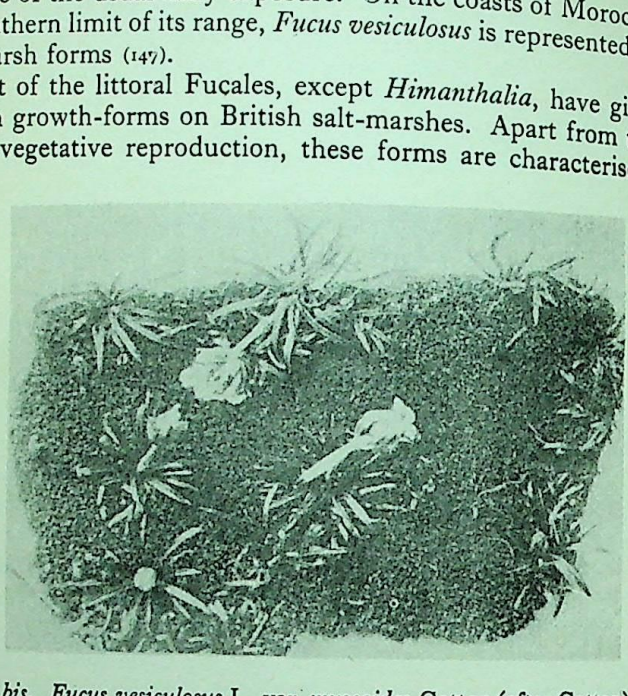

Fig. 137 *bis*. *Fucus vesiculosus* L. var. *muscoides* Cotton (after Cotton), sward-formation; intermingled are scattered plants of *Statice maritima*.

dwarf habit (fig. 138 F, G) and frequent spirality (fig. 138 A, B, G) or curling of the thallus. The dwarf habit has been attributed ((14) p. 357) to the greater degree of exposure (cf. however, (228) p. 68), and to the shorter period of immersion in sea water which is moreover often diluted. This factor is also believed to bring about the reduced width of the thallus, while spirality or curling has been ascribed to the reception of more moisture and nutritive salts by the side of the thallus adjacent to the mud during intertidal periods. A spiral form of *F. vesiculosus* has been obtained by placing plants entangled in wire-netting on a *Spartina*-marsh ((98) p. 63). No satisfactory explanation for the customary sterility has yet been afforded ((14) p. 364, (134) p. 144).

The salt-marsh forms of *Pelvetia canaliculata*, like the saxicolous form, occupy the upper levels and several different kinds have been

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distinguished ((13) p. 277, (29) p. 206, (159) p. 65, (249)). One of the commonest is that known as var. *libera* (fig. 138 E), which lies loose on the surface. The bushy plants are dark brown and copiously branched, the branches interlacing with those of adjacent plants so that a continuous covering is formed over the soil. In the rarer var. *coralloides* (cf. also (140) p. 280) the lower part of the thallus is embedded in the marsh, about 2 cm. projecting above the surface; it is more like the normal attached form and approaches the var. *radicans* found by Foslie ((56) p. 263) on the clay bottom of shallow rock-pools.

Ascophyllum nodosum is represented mainly by small forms of var. *scorpioides* ((14) p. 329, (139) p. 205), which is widespread in the loose-lying communities of the North Temperate zone (p. 387), and by a form known as var. *Mackaii* Cotton ((37) p. 128, (139) p. 202), which is sometimes ranked as a separate species (18). The latter (fig. 138 D) forms globular tufts which are often of some size and consist of a number of plants, with or without small air-bladders; it appears to arise directly by vegetative propagation from broken pieces of the ordinary lithophyte ((139) p. 203, (159) p. 67).

The forms of *Fucus* found on salt-marshes are very diverse and, although they are doubtless all derived by vegetative propagation from saxicolous types, the profound modification and the customary absence of fertile conceptacles make it difficult to establish their true affinities. In a survey of the British marsh-*Fuci* Baker and Bohling ((14) p. 330) refer most of them to *F. vesiculosus* (cf. also (212)) and class them in three groups—the relatively large spirally twisted ones (ecad *volubilis*, fig. 138 A), the turf like forms (ecad *caespitosus*), and the filiform ones (ecad *muscoides*); numerous transitional forms are recognised. Those placed in ecad *volubilis* (incl. *F. volubilis* Huds. and *F. lutarius* Kütz.) agree to a considerable extent with comparable ones (fig. 138 B) found on the continent (see below). The ecad *caespitosus* corresponds to the plant called *F. balticus* Ag. (*F. vesiculosus* var. *subecostata* Harv., *F. vesiculosus* var. *balticus* (Ag.) Cotton), and is common as an undergrowth in British salt-marshes ((37) p. 125, (139) p. 206). It is a dwarf, prostrate or erect, form showing little or no curling; the thallus is devoid of midrib and air-bladders, bears prominent marginal cryptoblasts, and the conceptacles sometimes show divided oogonia. The var. *muscoides* (fig. 137 *bis*; (37) p. 127, (139) p. 206) differs from this only in its erect growth and filiform fronds.

Sauvageau ((214), (215) p. 106, (229)), who undertook a detailed study of the French and Spanish salt-marsh *Fuci*, referred them to *F. lutarius* (Chauv.) Kütz. (*F. vesiculosus* var. *lutarius* Chauv.). The projecting part of the thallus (30–40 cm.) is narrow and spirally coiled (fig. 138 B), often devoid of air-bladders and provided with scattered cryptoblasts which are frequently marginal in position (fig. 138 C, *c*). The part buried in

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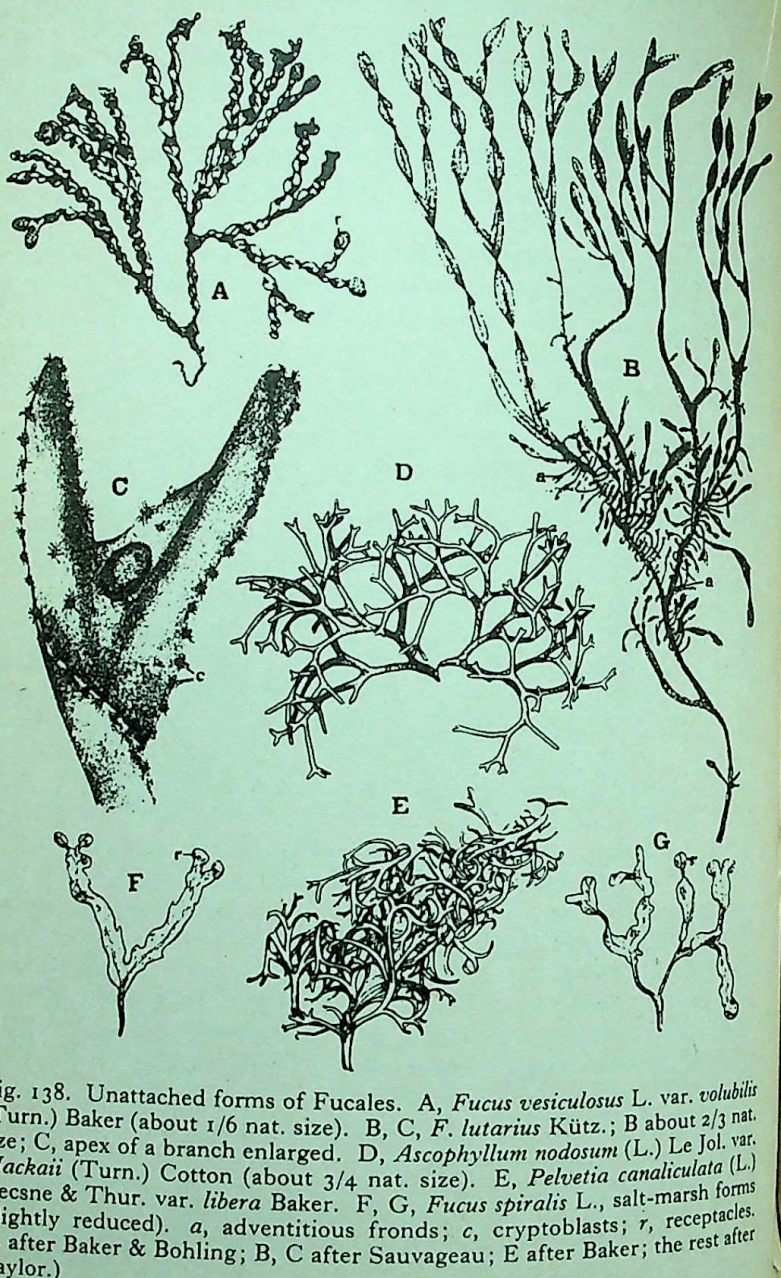

Fig. 138. Unattached forms of Fucales. A, *Fucus vesiculosus* L. var. *volubilis* (Turn.) Baker (about 1/6 nat. size). B, C, *F. lutarius* Kütz.; B about 2/3 nat. size; C, apex of a branch enlarged. D, *Ascophyllum nodosum* (L.) Le Jol. var. *Mackaii* (Turn.) Cotton (about 3/4 nat. size). E, *Pelvetia canaliculata* (L.) Decsne & Thur. var. *libera* Baker. F, G, *Fucus spiralis* L., salt-marsh forms (slightly reduced). *a*, adventitious fronds; *c*, cryptoblasts; *r*, receptacles. (A after Baker & Bohling; B, C after Sauvageau; E after Baker; the rest after Naylor.)

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the silt bears numerous small adventitious fronds (fig. 138 B, *a*) which, as they become free by decay of the stalk, bring about plentiful multiplication; they bear marginal cryptoblasts only. The rare individuals with fertile conceptacles are always female; the oogonia remain undivided, although several nuclei may be present. The receptacles are inflated with gas and adventitious fronds commonly arise from the edges of older conceptacles which have split open.

The spirally twisted *Fuci* of British salt-marshes were first ((13) p. 283; cf. also (139) p. 207) referred to *F. volubilis* Huds. which shows many similarities to *F. lutarius*. The plants (fig. 138 A) vary considerably in size and bear occasional oblong air-bladders; the rare receptacles display the features recorded by Sauvageau. The latter subsequently ((228) p. 70) referred the forms devoid of air-bladders to *F. lutarius* (cf. also (147)) and those possessing them to *F. volubilis*. Chemin ((32) p. 154) is of the opinion that the two sets of forms are not distinct.

Sauvageau ((228) p. 57) criticises Baker and Bohling's reference of the marsh Fucoids to *F. vesiculosus*. He argues that the sole presence of female plants is no proof of derivation from a dioecious species, since the special conditions might just as readily lead to abortion of the antheridia in a bisexual conceptacle as to the suppression of male plants (cf. also (170) p. 39). He is of the opinion that *F. lutarius* may have been derived from *F. spiralis*.

A remarkable silt-inhabiting form, growing to a length of 20–50 cm., has been described by Nienburg ((165), (166) p. 161, (170)) from the North Frisian "Wattenmeer" under the name of *F. Mytili*. Its sole anchorage is afforded by the byssus-threads of the Mollusc *Mytilus*. The plants, which show a tendency to twist and only rarely possess air-bladders, have plentiful cryptoblasts. Only female conceptacles with normal oogonia are present, but the packets of ova are not liberated. The receptacles proliferate into well-branched fronds which become free by decay, and this is believed to be the normal method of propagation ((170) p. 35). The parentage of this peculiar form is obscure, but it is possibly derived from *F. vesiculosus*.

Since the work of Baker and Sauvageau above discussed an undoubted limicolous form of *F. spiralis* has been recorded ((160) p. 431); the base of the small thallus (fig. 138 F, G) is embedded. Marsh-forms of *F. ceranoides* are also known ((14) p. 340, (160) p. 437, (250)), although *F. serratus* does not appear to be represented in such habitats.

Similar sterile unattached thalli of diverse Fucales often occur in huge numbers as loose-lying forms in the sublittoral region of the quieter land-locked seas ((209) p. 218, (231), (258) p. 35). They are derived from detached fragments, which have been carried by currents into these waters and there continue to propagate by vegetative means. One of the commonest forms appearing in this community in North Temperate seas is *Ascophyllum nodosum* var. *scorpioides* ((178) p. 41, (180) p. 66, (199) p. 33, (200) p. 7), in which the main axes are almost terete, devoid of air-bladders, and bear only occasional laterals; where

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such forms are not continuously submerged, they are much more compact and approximate to those found on salt-marshes ((37) p. 129, (139) p. 204, (272) p. 209).

Certain forms of *Fucus vesiculosus* play a very considerable rôle in the loose-lying communities of the Baltic ((134) pp. 60, 143, (238) pp. 35, 84; see also (8), (14) p. 338). Many of these, formerly grouped under *F. balticus*, show considerable parallel with the larger salt-marsh types, although they lack the characteristic spiral curling of the thallus. In the eastern parts of the Baltic, where the salinity becomes progressively lower, *F. vesiculosus* fruits more and more sparingly and is ultimately represented only by reduced vegetative forms ((71) p. 19, (106) p. 95, (113) p. 80, (313); cf. also (105) p. 657). Jónsson ((100) p. 19) records similar dwarf-forms of *F. inflatus* L. from East Greenland. A loose-lying form of *F. serratus*, found on muddy sand and shingle, has been recorded from Scotland (159). In the loose-lying community of the Adriatic ((231) p. 72) species of *Cystoseira* play an important part; the plants consist of detached axes covered with new proliferations.

The most striking of the unattached forms is the Gulf-weed which occurs in huge floating masses in the Sargasso Sea, off the African coast between 20° and 35° latitude N.; Parr (182) furnishes quantitative data. There is considerable evidence (cf. (24), (28), (80*a*) p. 54, (114), (115), (213), (294)) that these immense tracts of drifting *Sargassum* are formed by continuous vegetative reproduction *in situ* of occasional detached saxicolous individuals, carried there by ocean currents. The view, advocated especially by Kuntze ((118) p. 197; cf. also (246)), that this vegetation consists in the main of an accumulation of detached plants, has found little support in recent years. Attaching discs have never been found on the plants of the Sargasso Sea and investigation on the spot has shown that there is continuous growth of the younger parts, as the older die away. Hentschel (86) reaches the same conclusion by a study of the attached growth found on the Gulf-weed. Winge (294) and Sjöstedt (246) record a considerable increase in the amount of *Sargassum* during the summer, which the latter, probably wrongly, ascribes to the arrival of fresh plants from Central America and the West Indies. The newly detached individuals sometimes show fertile conceptacles with sex organs, but these appear to be functionless and, according to Winge, occur only in the westerly parts of the Sargasso Sea.

Boergesen ((24) p. 6) recognises two "species" in the Sargasso Sea, viz. *S. natans* L. (*S. bacciferum* C. Ag.) and more rarely *S. hystrix* J. Ag. var. *fluitans* Boerg. Both are sterile and exhibit attenuation and marked elongation of all the branches, as compared with the attached species of *Sargassum*. Winge distinguishes eight different types, of which only three are common. There is considerable resemblance between *S. natans* and certain of the attached West Indian species (*S. vulgare*, *S. Filipendula*), and Boergesen is of the opinion that one

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or other of these is possibly the parent from which the free-floating form is derived. Drifting specimens of *Sargassum* are very commonly encountered in the North Atlantic.

The difficulty of relating the diverse forms found in the Sargasso Sea to any of the known littoral species has led to the hypothesis that they might represent the remains of the littoral girdle of the continent of Atlantis ((68) p. 20). This conjecture, however, overlooks the profound modification which the detached lithophytic Fucales undergo in their adaptation to a loose-lying existence.

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Class X. RHODOPHYCEAE

The Red Algae fall naturally into two sub-classes, the Bangioideae and Florideae. The former include only a limited number of genera (Bangiales) which, although showing certain characters in common with the Florideae, exhibit so many significant differences that opinion remains divided as to their exact relation to the latter (p. 437). The bulk of the Bangioideae are marine, including such typical members of littoral vegetation as *Bangia* and *Porphyra*, but they also comprise a number of probably reduced freshwater and terrestrial forms. They provide the only examples of parenchymatous construction found among Rhodophyceae, and the broad expanses of *Porphyra* (fig. 142 A) constitute a remarkable parallel to those of *Ulva* and *Punctaria*.

In their diffuse growth they offer a sharp contrast to the Florideae which comprise the vast majority of the Red Algae. Growth is here effected by an apical cell which is commonly dome-shaped (figs. 151 A, *a*; 155 B, *ac*). Another characteristic feature, lacking in Bangiales, is constituted by the well-marked pits (fig. 139 B, *pi*), occupied by broad cytoplasmic strands, that occur in the septa between adjacent cells (p. 446). In the least specialised members of Florideae (*Acrochaetium*) the plant takes the form of a heterotrichous filament (fig. 148 A, B) and no simpler types of body are known. The heterotrichous filament is also encountered in *Erythrotrichia* and other Bangiales (fig. 142 G), while the freshwater and terrestrial members of the latter in part exhibit unicellular and colonial states (fig. 143 D, H, I, S) which are probably the result of reduction.

As in Phaeophyceae (p. 21), the heterotrichous habit is recognisable in the juvenile stages of most of the less specialised Florideae (Nemalionales, figs. 151 B; 153 C), although in the more advanced orders it is obscured and in the Ceramiales a prostrate system is no longer differentiated. The manifold types of thalli ((1) p. 5) exhibit varied degrees of compactness, but are invariably pseudoparenchymatous. They are composed of dense aggregates of the branch-systems of one (uniaxial types, fig. 154 C) or more (multiaxial types, fig. 158 D; 159 A) richly branched filaments which, in the heterotrichous forms, arise from the prostrate system. The resulting thalli are commonly cylindrical (fig. 163 B, C), with more or less copious ramification, although a marked foliaceous development occurs, for instance, in Gigartinaceae (fig. 174) and Delesseriaceae (fig. 192). Illumination may play a rôle in determining the organisation of the thallus ((7) p. 602). Morphological elaboration is far rarer than among Brown Algae and relatively few Florideae show complexities in outward form (cf. pp. 502, 568). The full consideration given to these matters on p. 450 et seq. renders a further discus-

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sion unnecessary. Few Red Algae attain to any considerable stature, although a considerable number are perennial in habit; a larger or smaller portion of the old frond usually persists and from it the new growth arises ((150) p. 235). Tissue-tensions, similar to those noted in Phaeophyceae, are occasionally manifest ((113) p. 834).

The vast majority of Florideae are marine and most of the fresh-water representatives (*Batrachospermum*, *Lemanea*, *Hildenbrandia*, see also (227)) belong to the less specialised groups; in general they favour well-aerated habitats (rivers and the littoral region of lakes). Many of the marine Florideae are sublittoral and normally inhabit deeper water and, when the latter is clear, can penetrate to very considerable depths ((16), (202) p. 177, (205) p. 483, (252) p. 135); such forms can only be obtained by dredging, unless cast up on the shore after storms. Certain Florideae (species of *Gigartina*, *Laurencia*, *Lomentaria*, etc.), however, form extensive belts in the littoral region and, where suitable substrata are available, Red Algae occur in this position even in the Tropics (234). On the other hand, many Florideae, found between tide-levels on temperate and other shores, are confined to the rock-pools and are evidently incapable of withstanding desiccation. A number (species of *Catenella*, *Bostrychia*, etc.) are adapted to life in brackish water, being characteristic members of certain types of salt-marsh vegetation and of the flora growing on the roots of tropical mangroves. Although distributed over the whole surface of the earth, the greatest abundance of Florideae is met with in the warmer seas (cf. (60) p. 281, (62) p. 281, (208) p. 329, (209) p. 99, (220) p. 298) and in Australasia.

The Rhodophyceae are distinguished by a complete absence of all motile stages, both the male cells and the diverse types of spores being devoid of organs of locomotion. There is indeed no evidence that motile types have ever occurred in this class, supposed flagellate representatives (e.g. *Rhodomonas*) having proved to belong to an altogether different affinity. One of the criteria that serves to demonstrate the homogeneity and probable separate origin of Chlorophyceae, Phaeophyceae, etc. is therefore lacking. On the other hand, all Rhodophyceae possess accessory photosynthetic pigments of a distinctive and similar kind, while the products of photosynthesis (Floridean starch, etc.) are equally characteristic. These features, taken in conjunction with the many striking morphological characteristics of Florideae (apical growth, filamentous construction, pit-connections), the universal oogamy and other marked peculiarities in the processes of reproduction (p. 599), all tend to suggest a common ancestry from which Bangioideae and Florideae probably diverged at a very early stage. The Red Algae exhibit no clear affinities with other classes and are commonly grouped as Rhodophyta, by contrast to the Chlorophyta, Chrysophyta, Phaeophyta, etc. Our knowledge of their fossil history is negligible (cf. (188) p. 96) and sheds no light on their

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evolution. The calcified Corallinaceae are met with from the Cretaceous onwards and have played an important rôle in the formation of limestone rocks (p. 511).

The Cell-wall

Two distinct layers are generally recognisable in the cell-wall ((1) p. 28). The inner, firmer layer adjoining the cell-cavity often consists largely of cellulose ((37) p. 142, (72), (110) p. 30, (122) p. 420, (247) p. 154, (253) p. 132; cf. also (175), (184)), while the outer layers are composed of pectic substances. In certain Florideae (*Cystoclonium*, *Gelidium*, *Laurencia*) the cell-walls are coloured blue by iodine ((94) p. 362, (108) p. 52) which Sauvageau ((203) p. 10) ascribes to the presence of amyloid; Hansen ((86) p. 284) records a red coloration of the middle lamella with iodine in species of *Gracilaria*. In the living cells of many Florideae the membranes are markedly stretched and compressed as a result of the turgor of the cell-contents so that, on treatment with hypertonic solutions, the shrinkage of the protoplast is accompanied by a decrease in the dimensions of the cell, as well as by a pronounced increase in the thickness of the wall ((96) p. 414, (97), (109) p. 125, (249) p. 150). This feature is responsible for the often considerable thickness shown by the cell-membranes in preserved material. The resulting difficulty in osmotic determinations by the plasmolytic method is met by Hoffmann (96) by utilising for such purposes the first indications of cell-shortening or membrane-swelling. According to Kylin ((135) p. 242) damaged cells of *Griffithsia* and of *Antithamnion plumula* exhibit an increase of the cell-wall to ten times its previous thickness. The "cuticle", apparent at the surface of some of the coarser forms, is probably a denser layer of pectic material; in some instances ((8) p. 5, (59) p. 24) it has been found to be resistant to strong acids.

Stratification of the membrane is very prominent in certain Ceramiaceae, where it has been studied as an example of growth by apposition ((212) p. 257, (230) p. 189). The classical instance is furnished by *Bornetia secundiflora* (fig. 139 A), where successive thickening layers (*i*) are deposited by the tip of the protoplast of the apical cell, while the outermost strata (*o*) are progressively burst; the wall thus comes to consist of numerous funnel-shaped pieces. A comparable stratification is recorded in species of *Antithamnion*, *Callithamnion*, and *Ceramium* (fig. 139 B, C; (10) p. 276, (187) p. 284). In cell-division the septa arise as annular ingrowths and show no relation to the nuclear spindle ((216) p. 222, (236) p. 227).

The pectic layers of the wall, which stain deeply with ruthenium red and methylene blue, at one time regarded ((122) p. 420) as calcium salts of pectic acids, are probably complex. They are either completely (*Rissoella*) or only partly (*Gelidium*) soluble in boiling water,

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and the solutions thus obtained are often spoken of as *geloses* (203). The products of their precipitation include the commercial agar-agar (derived from species of *Gracilaria*, *Gelidium*, and *Eucheuma*[1]) and carrageen (from *Chondrus crispus*[2] and *Gigartina stellata*). On hydrolysis these two substances afford galactose, accompanied by pentoses and possibly some glucose ((72), (85), (149), (158), (173) p. 303); Takahashi (237) obtained a sugar (floridose) from hydrolysed geloses of *Chondrus*, *Iridaea*, and *Ahnfeltia*. Agar and carrageen have also been shown to contain organically bound sulphur ((77), (149) p. 421, (176), (238)), and it is believed that they include calcium salts of ethereal sulphates (20, 84, 98); the gelose of *Ceramium rubrum* likewise contains an ethereal sulphate ((200) p. 585; cf. also (95) p. 294).

Kylin ((120) p. 194) distinguishes the geloses obtained from *Ceramium rubrum* and *Furcellaria fastigiata*, which readily solidify on cooling and are precipitated by ammonium sulphate, from those derived from *Dumontia incrassata*, which remain liquid on cooling and are not precipitated by the salt; carrageen resembles the former. Sauvageau ((203) p. 32, etc.) further differentiates between the geloses of *Gelidium*, *Gracilaria*, *Ahnfeltia*, etc., which solidify in the cold even in dilute solutions, and those of *Chondrus*, *Gigartina*, *Gymnogongrus*, *Hypnea*, etc., which only solidify when in concentrated solution or after treatment with electrolytes; that of *Polyides* is intermediate and its solution readily solidifies on addition of ammonium sulphate. Sauvageau states that in the seaweeds of the first group, which release their gelose at high temperatures without disintegration, the cellulose is very resistant to ammoniated copper oxide and amyloid is invariably present in the wall. According to Haas and Hill ((78) p. 358; cf. also (20)) carrageen is a mixture of two substances, the one soluble in cold water and producing a thick viscous solution not setting to a gel after boiling with a little Rochelle salt, the other soluble in hot water and readily affording a gel on cooling. The residue left after extraction contains cellulose.

Marked calcification of the cell-membranes occurs in Corallinaceae, as well as in species of *Peyssonnelia*, *Galaxaura*, and *Liagora* ((75) p. 534, (107) p. 147). According to Berthold ((6) p. 419) the envelope of lime is thicker in well-illuminated individuals. The incrustation first appears in the pectic layers and then penetrates into the cellulose layers, although the protoplast always remains enveloped by an uncalcified lamella. The lime takes the form of calcite in Corallinaceae (3), of arragonite in the others ((159) p. 51, (192)). Some magnesium carbonate is always present ((28) p. 48, (102), (142) p. 12, (143) p. 38), but in Corallinaceae this is only precipitated in the older thallus and in dead

[1] *Eucheuma speciosum* J. Ag. ((90) pl. 64) and *Gracilaria lichenoides* are used, like carrageen, in the preparation of jellies. *Ahnfeltia plicata* (245), *Pterocladia capillacea* (269), and others (271, 272) have been recommended as sources of agar.

[2] Regarding the collection and diverse uses of the products of *Chondrus crispus*, see (48) p. 681, (78) p. 353, (240) p. 142.

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parts(151). There is a greater proportion of magnesium in deep-water forms and little in those in which lime is deposited as arragonite. The amount of calcium and magnesium in *Corallina squamata* is greater in winter than in spring, but there is no constant relation between the two(82). Incrustations of carbonate of lime have been reported in freshwater forms ((242) p. 98, (248), (270)). Deposition of iron is recorded in *Batrachospermum* ((51) p. 51, (110)) and diverse other Red Algae ((162) p. 12, (225)).

The Protoplast[1]

The cytoplasm of diverse Florideae exhibits a high degree of viscosity and there is often a very firm adhesion to the wall ((99), (100), (135) p. 244, (244) p. 294), which is stated ((19) p. 449) to be due to extension of the protoplast into the innermost layers of the membrane. These features are no doubt related to the fact that the protoplast, during plasmolysis ((101) p. 384, (251)), remains in contact with the wall at diverse points and develops concave contours which are irreversible (fig. 139 R). Such phenomena are not shown by all the species that have been investigated and the extent of their occurrence is not at present clear; the published data refer mainly to Ceramiales.

The protoplasts of Florideae are commonly killed by plasmolysis ((12), (52) p. 105, (125) p. 381, (135) p. 245), *Heterosiphonia plumosa* being specially susceptible, while *Ceramium ciliatum* ((100) p. 67) and *Callithamnion corymbosum* ((52) p. 99), for instance, are more resistant; capacity to resist hypertonic solutions is stated to run markedly parallel with cold resistance ((100) p. 69). Many Red Algae are also very sensitive to dilution of the medium ((100) p. 60), although *Antithamnion cruciatum* and *A. spirographidis* (256),[2] for example, are less sensitive than others. The harmful effects of dilution of the medium on Florideae are also shown by the marked diminution in number, as well as in the size and degree of branching of the surviving forms, in seas with lower degrees of salinity (cf. (199) p. 41, (224)).

Diverse Ceramiales are stated (13) to show marked susceptibility-gradients to hypo- and hypertonic sea-water, as well as viscosity-gradients (cf. also (26), (101) p. 379, (263)). In general the older cells show a higher degree of viscosity than the younger, but in *Cryptopleura*, for instance, this is more marked in the marginal cells. It is evident, however, that the protoplast does not always possess a high viscosity. Thus, in certain Ceramiaceae (*Callithamnion*, *Monospora*) the cross-walls of the older cells bear aggregations of cytoplasm from which numerous processes, exhibiting constant change of form, extend into the vacuole ((25) p. 173, (160) p. 289, (186)).

[1] Certain special features of the protoplast (light-reflecting bodies, vesicular cells) are considered later (p. 584 et seq.).

[2] Miranda ((161) p. 378) suggests that the form studied by Westbrook is *Antithamnionella*.

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The contents of the vacuoles show an alkaline, neutral, or acid reaction ((2), (122) p. 349, (137) p. 8), while the expressed sap is acid (27); aqueous extracts exhibit a *p*H ranging between 4·0 and 6·8 ((136) p. 646). The contents of the vacuoles readily take up stains like neutral red or cresyl blue (191) which commonly results in the formation of crystalline precipitates ((24) p. 165, (137) p. 8, (190)). The osmotic pressure is in general rather lower than that of Phaeophyceae or Chlorophyceae ((135) p. 242); according to Biebl ((12) p. 414, (14) p. 352) it is lower in deep-water (1·5 times that of sea-water) than in littoral forms (2·0–2·2 times that of sea-water) and in general corresponds with that of the strongest hypertonic solutions that can be withstood without injury. In *Ceramium ciliatum*, which is more resistant to plasmolysis than other littoral forms, the osmotic value of the sap approaches that of the permanently submerged forms.

Chromatophores and Pigments

A single chromatophore, which is usually axile and more or less stellate in form, is characteristic of many Bangiales (figs. 139 P; 143 B, R) and a comparable condition is met with in diverse Nemalionales. In the peripheral cells of *Nemalion*, *Helminthocladia* (fig. 159 B, *c*), *Liagora*, etc. the chromatophore, which lies adjacent to the outer walls, is asymmetric, the internally directed processes being more strongly developed ((197) p. 147, (206) p. 38, (214) pp. 19, 63); such chromatophores have also been recorded in *Acrochaetium* ((67) p. 371, (214) p. 19). The processes arising from such axile chromatophores commonly broaden at their periphery (fig. 139 P, *pe*; cf. Desmids, I, p. 344), and in elongate cells these parietal enlargements may become band-shaped and assume very irregular shapes, sometimes forming an almost continuous layer ((259) p. 610). The occurrence of parietal chromatophores in diverse Bangiales (fig. 139 H) and Nemalionales (Naccariaceae; *Scinaia*, fig. 159 E, *c*; *Batrachospermum*) suggests a possible derivation of the parietal from the axile type by elimination of the central body of the chromatophore.

It is essentially in the forms possessing axile chromatophores that the spherical bodies known as *pyrenoids* ((39) p. 207, (112) p. 327) occur, although they are also found in the parietal chromatophores of some species of *Acrochaetium* (fig. 148 F, *p*) and *Rhodochorton* (fig. 149 C–E, *p*; (111)); they are not, however, present in all Bangiales and Nemalionales. Like the pyrenoids of Chlorophyceae they constitute denser parts of the chromatophore, but they do not show the same contraction on fixation and do not stain so deeply; moreover, although grains of Floridean starch are sometimes grouped around the pyrenoids (fig. 139 P, *s*), there does not appear to be direct contact and the relation is not so definite as in Green Algae. In *Nemalion* and *Helminthocladia*, Schmitz ((214) p. 63) records pyrenoids also within the processes of the chromatophore and believes that these arise *de novo*.

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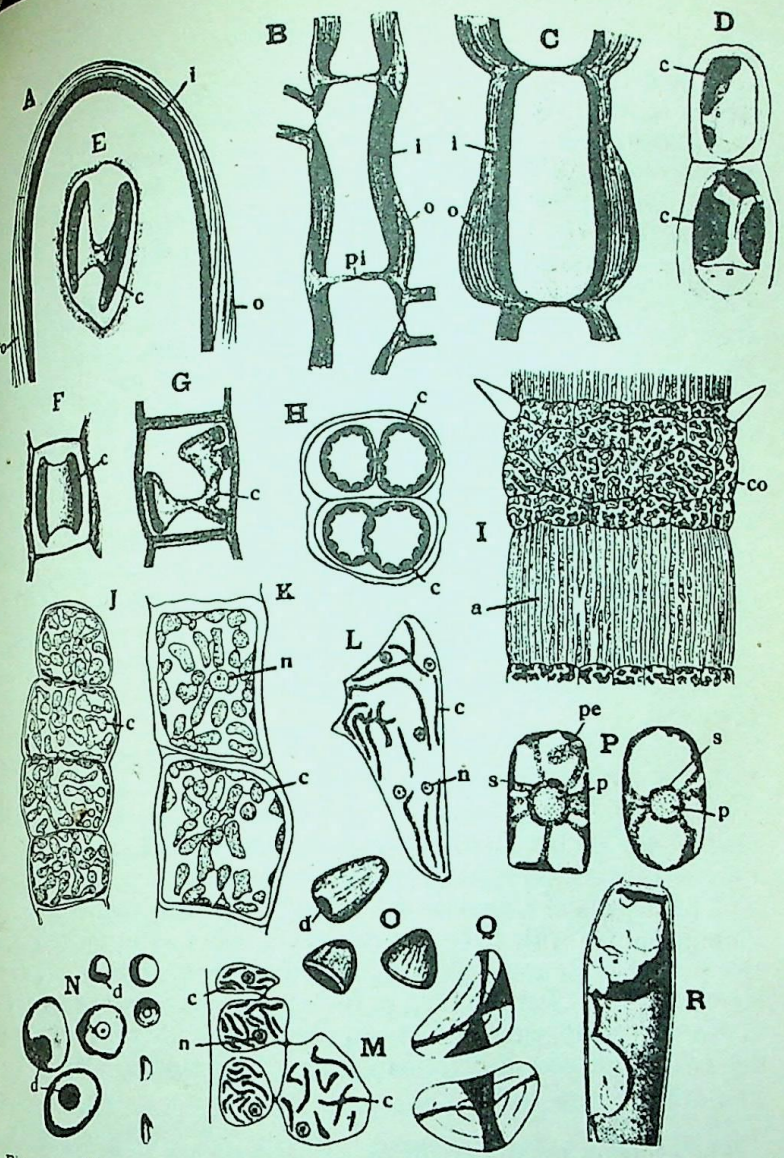

Fig. 139. Chromatophores, etc. of Rhodophyceae. A–C, structure of cell-membrane; A, *Bornetia secundiflora* (J. Ag.) Thur.; B, *Callithamnion thuyoides* (Engl. Bot.) Ag.; C, *Antithamnion cruciatum* (C. Ag.) Naeg. D–M, P, chromatophores; D, *Chondrus crispus* (L.) Stackh.; E–G, *Phyllophora membranifolia* (G. et W.) J. Ag.; H, *Rhodospora sordida* Geitler; I, *Ceramium* sp.; J, K, *Asparagopsis armata* Harv.; L, M, *Cystoclonium purpureum* (Huds.) Batt.; P, *Asterocytis smaragdina* Reinsch. N, O, Q, Floridean starch; N, *Ptilota plumosa* (L.) Ag.; O, *Gracilaria dura* (Ag.) J. Ag.; Q, grains of Floridean starch viewed in polarised light. R, *Griffithsia*, part of a plasmolysed cell. *a*, axial cell; *c*, *pe*, chromatophores; *co*, cortex; *d*, depression on starch-grain; *i*, inner and *o* outer strata of wall; *n*, nucleus; *p*, pyrenoid; *pi*, pit; *s*, starch-grains. (A after Strasburger; B, C after Berthold; D–G after Darbishire; H, P after Geitler; I after Schimper; J, K after Svedelius; L, M after Kylin; N after Bruns; O after Hansen; Q after Czurda; R after Höfler.)

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A single large parietal chromatophore is found in the photosynthetic cells of certain of the more specialised Florideae, for instance in *Hildenbrandia*, *Agardhiella* ((183) p. 410), *Dumontia* ((54) p. 437), *Polyides* ((47) p. 11), *Chondrus* (fig. 139 D), and *Phyllophora* (fig. 139 E–G). In the older cells such chromatophores often become lobed or divided (figs. 139 G; 254 I, *c*) and in *Polyides* they break up into a number of band-shaped structures. More usually the cells of Florideae contain considerable numbers of parietal chromatophores from the first. Where recognisable (*Callithamnion*, *Spermothamnion*) they appear within the apical cells as lenticular discs, although in many Florideae (e.g. *Polysiphonia*, *Ceramium*) these cells are almost colourless ((206) p. 42, (214) p. 87). The lenticular form may be retained in the mature cells, as in many Delesseriaceae (fig. 190 B), Corallinaceae ((198) p. 212), diverse Ceramiaceae ((214) p. 11), etc., and in such instances the chromatophores are usually numerous. Commonly, however, they are fewer and irregularly lobed (*Asparagopsis*, fig. 139 J, K) or band-shaped (e.g. *Furcellaria*, *Cystoclonium*, fig. 139 L, M), contiguous ones often fitting closely together. In diverse Ceramiales ((214) p. 83) and in *Lemanea* (152) the rounded chromatophores of the apical cells develop into ribbon-shaped ones which may be lobed or branched.

The shape of the chromatophores often depends on that of the cell and may vary appreciably in different cells of the same individual. Thus, in the cortical bands of *Ceramium* (fig. 139 I, *co*) the chromatophores are irregularly shaped and almost isodiametric, while in the axial cells (*a*) they appear as elongate ribbons ((114) p. 223, (206) p. 43). The branchlets of *Crouania attenuata* ((15) p. 231) contain a parietal chromatophore with irregular processes, whereas in the axial cells there are delicate and widely separated ribbons. Similar differences are described by Berthold ((9) p. 6) between the outer and inner cells of diverse Cryptonemiales. Movements of the chromatophores under different conditions of illumination have been studied in a number of Florideae (cf. (219) and p. 584).

The evidence for the origin of chromatophores from mitochondria (177) is inconclusive. In the fertilised carpogonia of *Lemanea* and other Florideae Mangenot ((152), (154) p. 195; cf. also (23)) records decrease in size of the chromatophores followed by fragmentation and discoloration which results in the formation of a quantity of rods and granules; similar bodies are found also in the young carpospores, but during germination some of them enlarge and, acquiring pigment, give rise to chromatophores. Comparable changes probably occur in many Florideae, although the carpogonia often lack pigmented chromatophores already before fertilisation.

The substance of the chromatophores is semi-fluid ((10) p. 173, (11), (114) p. 230, (145) p. 89) and under certain circumstances they exhibit amoeboid changes of form and undergo fusions. They are readily

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affected by dilution of the surrounding medium ((12) p. 397). The green colour, which is usually assumed by Red Algae when boiled in distilled water and which is due to alteration of the phycoerythrin, is ascribed to the alkaline reaction of the chromatophores ((136) p. 648).

The coloration of the chromatophores[1] is largely due to two water-soluble pigments, the red *phycoerythrin* and the blue *phycocyanin* which obscure the other pigments. Chlorophyll *b*, if present at all, is found only in small traces ((129) p. 45, (222) p. 78, (228) p. 458), while both carotene and xanthophyll are present ((117) p. 113, (267) p. 241). Recently ((92), (129) p. 48, (138) p. 7) it has been shown that there are a number of carotenoid pigments. The chlorophyll-content is comparatively low (146-8), although, like that of phycoerythrin, greater in deep water and feebly illuminated forms which also show an increased ratio of phycoerythrin to chlorophyll (146, 147). The chlorophyll-content is stated to be higher in arctic types (103). The normal sterol of Rhodophyceae is sitosterol, but this is not without exception ((22) p. 106); *Polysiphonia nigrescens* is stated to contain fucosterol. Flavin ((250) p. 258) is widely represented, especially in *Iridaea*.

The accessory pigments, which resemble those found in Myxophyceae (p. 781), are of the nature of proteins[2] and show characteristics similar to those of globulins ((116) p. 235, (140), (163) p. 181, (164)). They can be extracted from fresh material by prolonged treatment with distilled water, although the pigments of certain Florideae (*Griffithsia*, *Phyllophora nervosa*; (86) p. 296, (118) pp. 398, 420, (140) p. 78) only pass very slowly through the cell-membranes. The phycoerythrin is precipitated from the solution by addition of crystallised ammonium sulphate and purified by repeated recrystallisation. Further fractional precipitation of the original solution gives phycocyanin in a crystalline form. The pure solution of phycoerythrin is carmine red and shows a marked orange-yellow fluorescence in reflected light (cf. also (217) p. 305), while that of phycocyanin is indigo blue and exhibits dark red fluorescence (cf. also (49), (116) pp. 186, 213). In certain Rhodomelaceae, with a red or reddish-brown colour (e.g. *Rhodomela subfusca*, *Polysiphonia nigrescens*), the phycoerythrin-solution shows only a faint fluorescence ((69) p. 191, (118) p. 423, (119) p. 532, (132) p. 3, (233) p. 4004) which has been ascribed ((22) p. 106, (140) p. 78) to admixture of brown pigments, although this is disputed by Kylin.

The crystals of phycoerythrin are hexagonal prisms ((116) p. 187, (163) p. 179), while those of phycocyanin are rhombic plates ((164)

[1] See (134) p. 14, where the older literature is mentioned.

[2] Hanson (87) disputes this for phycoerythrin, but it is very doubtful whether he worked with pure material (cf. also Molisch in *Zeitschr. Bot.* **2**, 357, 1910). Lubimenko (147), finding that the ratio between chlorophyll and phycoerythrin changes by a definite multiple in deep-water forms, concludes that they are chemically allied and that only one natural pigment is present (cf. also (31) p. 25).

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p. 133). Crystals of phycoerythrin (the *rhodospermin* of Cramer (38); cf. also (86) p. 301, (104) p. 290) and phycocyanin ((118) p. 422) are sometimes found in dead cells. Both chromoproteins consist of a colour- and a protein-component ((116) p. 236, (141)) which can be separated by treatment with acids or alkalis. The pigments are decomposed by strong light, but phycocyanin is more susceptible than phycoerythrin. Both the total amount and the relative proportions of the two pigments vary in different seasons, but these variations do

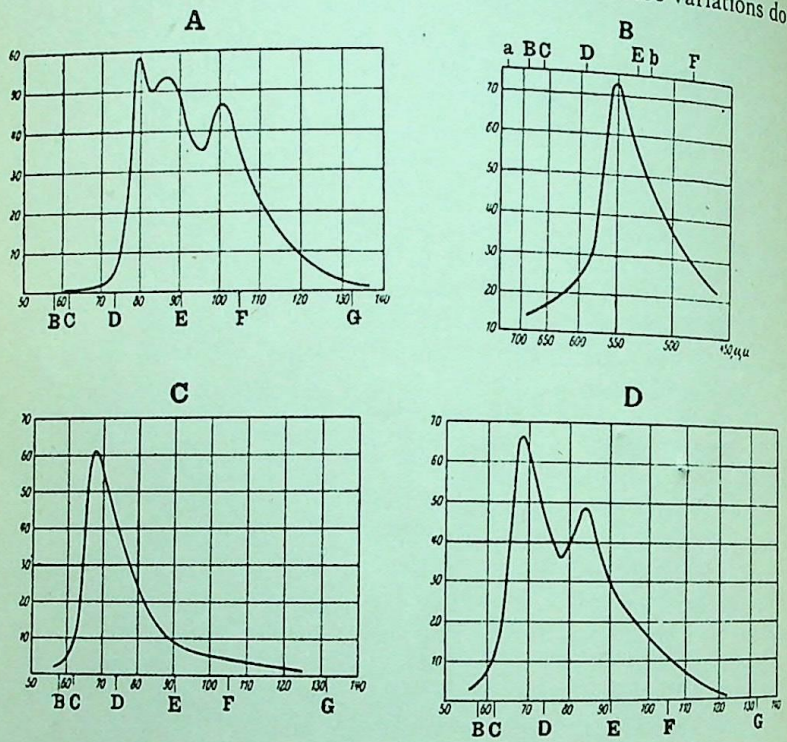

Fig. 140. Absorption-spectra. A, phycoerythrin of Rhodophyceae. B, phycoerythrin of Myxophyceae. C, blue-green phycocyanin. D, blue-violet phycocyanin. (B after Boresch; the rest after Kylin.)

not depend only on changes in light-intensity ((60) p. 86, (116) p. 233, (140) p. 53).

The solutions of phycoerythrin and phycocyanin afford characteristic spectra (cf. also (42), (196) p. 204). That of the former (fig. 140 A) normally shows three absorption-bands, which are situated in the green and blue between the lines D and F; in *Sebdenia Monardiana* there are only two bands ((63) p. 88, (195) p. 88, (233) p. 4005). Two modifications of phycocyanin have been distinguished in Florideae ((42), (116) p. 229, (118) p. 423, (132) p. 5, (165), (229) p. 38), viz. a bluish-violet one extracted from *Ceramium rubrum*, with two absorption-

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bands in the orange-yellow and green between the lines C and E (fig. 140 D), and a blue-green one extracted from *Batrachospermum* and *Lemanea*, with only a single absorption-band in the orange-yellow between the lines C and D (fig. 140 C); the latter is widely distributed in the Blue-green Algae.

The brilliant red colours exhibited by deep-water Florideae are, according to Kylin ((119) p. 536, (132); cf. also (233) p. 4005), conditioned by the presence of considerable amounts of phycoerythrin, while phycocyanin is lacking. The diverse (cf. also (6) p. 416, (62) p. 238) shades of purple, dark brownish-red, reddish-violet, or violet exhibited by the littoral forms are, on the other hand, ascribed to increasing admixture of phycocyanin. The red-violet littoral form of *Chondrus crispus* contrasts with the bright red submerged form which lacks phycocyanin ((118) p. 405). A high proportion of the latter is met with in *Gigartina stellata* and *Rhodymenia palmata*. Many littoral Rhodophyceae at times exhibit brownish, greenish or yellowish tints. The freshwater Florideae (*Batrachospermum*, *Lemanea*), which in general show dark green or blue-green colours, nevertheless contain both pigments ((118) p. 397), a reddish coloration becoming apparent after death or when the alga is grown in the shade (71); *Asterocytis ornata* and some *Batrachospermums* (e.g. *B. vagum*) are, however, believed to lack phycoerythrin. Heilbronn (93) has shown that the depth of coloration of *Sphaerococcus* depends on the intensity of the light.

Many Florideae are very sensitive to light-intensities higher than those obtaining in the deep-water habitats which they normally frequent[1] ((6) p. 415, (178) p. 288, (179) p. 406, (182) p. 385); a number of such seaweeds often flourish in caves and other feebly lighted situations in the littoral region ((115) p. 223, (169), (201), (205) p. 485). It is evident, however, that by no means all Red Algae are shade-forms, as little as all marine Chlorophyceae are sun-forms. Apart from the data already given (cf. pp. 4, 398), it may be noted that certain Rhodophyceae (*Bangia*, *Porphyra*, *Endocladia*, some *Polysiphonias*) are specially characteristic of the upper zones of the littoral region, while others can thrive in shallow moving water in the strong light of the Mediterranean summer ((6) p. 416). Svedelius ((234) p. 200) describes how diverse Red Algae (especially *Rhodomela crassicaulis* Harv., *Corallopsis Opuntia* J. Ag.) are exposed on the coral-reef at Galle in Ceylon without apparent damage (cf. also (15) p. 488, (239) p. 117). The recent researches of Montfort ((167, 169); cf. also (139)), moreover, show that the same species can exist in different light-habitats, the photosynthetic capacities being adapted in each to the prevailing light-intensity. Even among shade-forms there are marked

[1] For the rate of reduction of the light-intensity in sea-water, with increasing depth, see (2a), (29), (106) p. 230, (189), (221) p. 597, (223) p. 155 and other literature there cited.

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differences in the power of accommodation to stronger light ((171) p. 54).

Investigations of photosynthesis at diverse depths of submergence ((66) p. 184, (167), (168), (246)) or in light of different intensity ((63), (172), (194) p. 287) demonstrate that deep-water (shade) forms among Rhodophyceae carry on appreciably more photosynthesis in feeble light than sun-forms like *Fucus vesiculosus* and green littoral types (species of *Cladophora*, *Enteromorpha*, etc., cf. also (56) p. 840). On the other hand Red Algae from well-lighted habitats have, in the natural illumination of deep water, no advantage over shade-forms among Chlorophyceae ((170a) p. 547), while shade-forms among Phaeophyceae (*Dictyota*, *Desmarestia* (66) p. 186) do not differ appreciably in their capacity for photosynthesis, under such circumstances, from Red Algae belonging to the same horizons. Red Algae rich in phycocyanin make a better use of stronger light than those poor in this pigment. The lower limits to which the permanently submerged forms can penetrate must of course depend on their compensation points, which in turn are in large part dependent on constitutional features. The absolute value for photosynthesis in *Gigartina Harveyana* is stated to be not far below that obtained with leaves of *Helianthus* (56).

Since Engelmann (57), with the help of his bacterial method, concluded that Algae synthesise best in light of the complementary colour, this question has been the subject of repeated investigation. Engelmann himself ((58) p. 91) found that Red Algae, illuminated by a projected microspectrum, exhibit maximum photosynthesis in the green, and this has since been corroborated by diverse other experimental methods. Thus, Richter ((194) p. 285), determining photosynthesis by the amount of oxygen produced, established that Red Algae (*Callithamnion*, *Delesseria*) were more efficient in green light than Chlorophyceae from the same horizons (cf. also (195)). Wurmser (260), estimating photosynthesis in red, green, and blue light of known energy-value by the colorimetric method,[1] found that *Rhodymenia palmata* exhibited more photosynthesis in green light than *Ulva Lactuca* (cf. also (264)). Ehrke (55) compared the photosynthesis of *Enteromorpha compressa* and *Delesseria sanguinea* in weak light of different wave-lengths but equal intensity and arrived at the conclusion that the green alga exhibited maximum photosynthesis in red and the red alga in green light (cf. also (56) p. 839, (148), (210) p. 568). Red Algae also photosynthesise more strongly than Brown (*Dictyota*) in green light ((170a) p. 522).

According to the theory of complementary chromatic adaptation (64) the broad distribution of Green, Brown, and Red Algae, at progressively lower levels on the shore, is an outcome of the chromatic adaptation of the two last to the special colour of the light to which

[1] The methods are criticised by Harder (*Zeitschr. Bot.* 15, 359, 1923).

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they are normally subjected; owing to differential absorption of the rays of different wave-lengths there is, in deeper water, an almost complete elimination of the longer ones ((2a) p. 149, (73), (221) p. 598). The littoral Phaeophyceae do not fit into this picture at all, although the possession of fucoxanthin, with its capacity for absorbing blue rays, probably gives such forms as can exist in deep water some advantage (p. 31). The discussion of the theory of chromatic adaptation, so far as it concerns seaweeds, has in fact mainly centred about the Rhodophyceae. A considerable number of these, however, frequent the littoral region. Moreover, the evidence that Red (or Brown) Algae possess the capacity to adopt a colour complementary to that of the incident light, such as is established for certain Blue-green Algae (p. 783), is altogether inconclusive ((93) p. 8, (179) p. 433). Gaidukov's ((65); cf. also (174)) contention that the green colour assumed by *Porphyra laciniata*, after exposure to strong red light for 19 hours, is an example of such adaptation, is erroneous, since the colour-change no doubt depends on decomposition of the accessory pigments (cf. (134) p. 20, (201)). Such green-coloured Rhodophyceae (*Chondrus*, *Gigartina*, *Laurencia*) are not uncommonly found in the littoral region (cf. (88) p. 348, (174), (193) p. 89, (208) p. 331), their photosynthetic efficiency in strong light being less than that of the accompanying Chlorophyceae (170) or corresponding submerged forms.

Richter (194) was the first to point out that the littoral Red Algae do not exhibit the greater photosynthetic efficiency in green light shown by sublittoral types, and this has been fully corroborated by Montfort (170a). Richter's results led him to deny all participation of the accessory pigments of Rhodophyceae in photosynthesis, the superiority shown by sublittoral forms being ascribed solely to a higher capacity for utilising the available light. It cannot be doubted, however, that the accessory pigments of the numerous Red Algae, that flourish in the greenish-blue light of deeper water, will confer a decided advantage upon them with respect to light-absorption (cf. (221)). It is still, however, a debated question how far their more efficient photosynthesis is due to increased capacity for light-absorption ((17) p. 56, (63), (89) p. 348, (172) p. 43, (195)) or how far it is due to a "plasmatic" factor allowing of a more efficient use of the available energy ((169), (171) p. 52). Diverse authorities ((55) p. 663, (89) p. 348, (182) p. 385) are of the opinion that both factors are involved, while some consider that the accessory pigments act as photosensitisers ((87) p. 340, (119) p. 543, (134) p. 21, (140) p. 54). The dark-violet shade-inhabiting Florideae can also use yellow light for photosynthesis ((170) p. 201).

The Photosynthetic Products

The characteristic photosynthetic product in Rhodophyceae is a polysaccharide, usually spoken of as *Floridean starch*, which occurs abundantly in certain cells in the form of small solid grains ((5), (18)

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p. 173, (196) p. 218, (214) p. 151). Some of these, generally of smaller dimensions, lie free in the cytoplasm, whilst others are apposed to the chromatophores, although never deposited within their substance; in *Phyllophora* ((43) p. 23) and *Chondrus* ((44) p. 20) Darbishire records their formation in contact with leucoplasts (cf. however (247) p. 153). A direct participation of the chromatophores in the formation of the grains is denied by some ((5) p. 226, (155), (206)), but this is not the general opinion, although it remains uncertain whether the free grains arise within the cytoplasm itself ((39) p. 205, (207) p. 88) or are such as have become detached from the surface of the chromatophores ((94) p. 365, (120) p. 190, (134) p. 2). The grains are sometimes aggregated around the nucleus (I, fig. 2 H; (155), (214) p. 153) and this has been regarded as the normal seat of their formation. Where pyrenoids occur, the starch-grains are often distributed around them (fig. 139 P_5; (67) p. 369), and such pyrenoid-starch may possess a greater degree of permanency than the rest.

The larger grains are commonly basin-shaped (fig. 139 N) or conical (fig. 139 O), with an obvious depression (*d*) on one surface ((18) p. 174, (86) p. 285, (94) p. 365) which is regarded ((120) p. 190) as marking the point of contact with the chromatophore; Mangenot (155) also records irregular polyhedral shapes. An occasional faint stratification (fig. 139 Q) is evident, while the radial splits which appear on the application of slight pressure indicate a possible sphaeritic structure. The grains exhibit marked double refraction, showing a dark cross (fig. 139 Q) when viewed between crossed Nicols (241). They swell readily in hot water, potash, chloral hydrate, and iodine reagents. Grains, swollen by prolonged treatment with the last, often show differentiation into a central, more deeply stained, and a peripheral lighter-coloured region ((18) p. 175). According to Oltmanns ((182) p. 204; see also (47) p. 14) the latter is surrounded by a single or double ring of rounded granules, a fact which led him to suggest that the central region might be of the nature of a pyrenoid; it is difficult to find any support for this view (cf. (39) p. 209).

On treatment with iodine-solution ((18) p. 175) the grains are at first coloured yellow or yellow-brown, but, as swelling sets in, the tint changes to red, red-violet, or blue. If swelling is previously induced by treatment with hot water or chloral hydrate, violet or blue shades appear at once with iodine ((108) p. 36); occasional direct coloration, after treatment with chloral hydrate (e.g. in *Spermothamnion Turneri*), is no doubt due to the iodine-content (p. 587) of the alga. The colour assumed with iodine-reagents varies considerably, both in different species and in one and the same species ((94) p. 366), but the deep blue shades typical of the starch-grains of higher plants are not often obtained, the most frequent tints being red or reddish-violet; Mangenot (155) also records brownish shades. While Kolkwitz ((108) p. 35) concluded that there was no essential difference from the starch of other plants and Bruns ((18)

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p. 177) regarded Floridean starch as equivalent to the so-called red starch found in *Myristica*, etc., Schimper ((207) p. 88) denied any close relation between it and that of other groups. Belzung ((5) p. 223) was of the opinion that it consisted largely of amylodextrin, while Mangenot (153, 154) recognises a resemblance to glycogen. The evidence seems to indicate that it is a substance allied to, but not identical with, the starches of higher plants ((21), (120) p. 190, (134) p. 24, (166) p. 389).

Kylin ((120) p. 191) showed that the starch, removed from *Furcellaria fastigiata* by mechanical means, gives dextrose on hydrolysis with weak acids, while treatment with malt diastase results in the formation of sugars. Bartholomew ((4); cf. also (46)) extracted from diverse Red Algae a diastase which digests maize-starch, although more slowly than ordinary diastase. The starch is no doubt a reserve-substance (108); this is shown *inter alia* by its marked accumulation in perennating structures (e.g. the midrib of *Delesseria*, p. 534) and its decrease on the resumption of growth ((70) p. 260).

The nature of the primary product of photosynthesis in Red Algae still remains uncertain, although Kylin ((122) p. 355, (127) p. 243) believes he has established by macrochemical means the presence of small quantities of dextrose (cf. however (32) p. 154). Mannitol, commonly found in Phaeophyceae (p. 33), does not occur in Red Algae ((76) p. 53, (81) p. 61, (127) p. 243), but other sugar alcohols (dulcitol, sorbitol) have been demonstrated in *Bostrychia* (79, 80) and *Iridaea* (91). Alcoholic extracts of Florideae (especially of *Rhodymenia palmata* which contains little starch) are dextrorotatory and, when concentrated, have a sweet taste ((34), (122); cf. also (218) p. 103); after treatment with strong acids they reduce Fehling's solution. Such extracts have afforded crystals of a galactoside of glycerol ((32), (36), (76) p. 63) which has been named *floridoside* (cf. also (81, 81*a*)). This substance may constitute another food-reserve. In *Rhodymenia palmata* its accumulation begins in May and increases to a maximum in summer (35), while in *Corallina squamata* (82) it is highest towards the end of May and least at the end of January. *Lemanea* is stated (33) to contain trehalose, as well as floridoside and a glycogen-like substance. Kylin ((122) p. 350) records oxalates in diverse Florideae, and crystals of calcium oxalate have been observed in the axial cells of *Spyridia* ((104) p. 315). Fats do not appear to occur in any considerable quantity in Red Algae ((81) p. 58).

Nitrates can be demonstrated in many Rhodophyceae, often especially in the older parts ((122) p. 340, (231) p. 84, (232) p. 108), although lacking in some (*Polysiphonia*); in *Ceramium rubrum* they make up 1·5% of the dry weight. Haas and Hill ((81) p. 65, (81*a*), (82), (83)) find an accumulation of pentapeptides in Corallinaceae and *Griffithsia* and suggest that their presence may be due to a lack of balance between carbon and nitrogen metabolism owing to the depression of photosynthesis as a result of low light intensity. Crystal-

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loids (fig. 147 N, *cr*), probably composed of proteins, are not uncommonly found floating in the cell-sap ((104) p. 290, (105), (268) p. 184), although stated ((40), (61) p. 10, (185) p. 2) to lie in the cytoplasm in *Ceramium* and *Monospora*. Lewis ((144) p. 649) records rounded protein-masses in *Griffithsia*.

Although no generalised statement is possible in the present state of our knowledge, it is clear that the metabolism of Rhodophyceae differs appreciably from that of other algal classes. This is perhaps also shown by the frequent deposition of iodine-compounds in special cells (p. 586). Vitamins (265, 266) are specially abundant in *Porphyra*.

The Nucleus

The cells of the less specialised Rhodophyceae (Bangiales, Nemalionales) are always uninucleate ((134) p. 5, (211)) and this is also so in many Cryptonemiales (e.g. *Dumontia*, *Polyides*, *Gloeosiphonia* ((9) p. 7) and Gigartinales (e.g. *Furcellaria*, *Calosiphonia*). In other instances the older cells are multinucleate (Gelidiales, Rhodymeniales, many Ceramiales), while in *Griffithsia* and *Bornetia* this is even true of the apical cells. The number of nuclei is by no means always proportional to the size of the cell ((213) p. 123); in *Plocamium* ((128) p. 51), for instance, the axial cells contain a single huge nucleus, 30–35 μ in diameter, whilst the surrounding cells possess a number of small ones (cf. also (128) pp. 86, 111). The axial cells of Ceramiaceae, however, contain larger nuclei than the peripheral cells ((204), (257) p. 571). The diverse types of reproductive cells are invariably uninucleate.

The resting nuclei of the vegetative cells are for the most part of small size, with an average diameter of 3 μ ((134) p. 6); in some species (*Chondrus crispus*, *Calliblepharis ciliata*) they are exceptionally minute ((254) p. 151). According to Svedelius ((235) p. 310) the nuclei of tetrasporangiate plants of *Delesseria sanguinea* are larger than those of sexual plants, but this does not appear to be a general rule. The nuclei[1] exhibit a prominent nucleolus (sometimes several) and a well-developed network with numerous chromatin grains (fig. 141 A), although the chromatin-content is often rather scanty. Nuclei of irregular shape have been recorded in some Ceramiales ((204), (235) p. 306).

At the commencement of mitosis[2] the nucleus enlarges, the chromatin grains increase in size and decrease in number, probably as a result of fusion (fig. 141 B, C, O, P), and the network is often described as coarser. The chromatin grains are frequently arranged in rows (fig. 141 L), but no typical spireme has been recorded. At the end of prophase the short, and commonly in great part rounded,

[1] See (53) p. 553, (121) p. 39, (123) p. 101, (128) pp. 25, 71, 87, (185), (235) p. 307, (254) p. 151, (255), (261) p. 403, (262) p. 91.

[2] For meiosis, see p. 604.

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chromosomes are constituted (fig. 141 F, R, *c*). The spindle is intranuclear in *Polysiphonia* (fig. 141 E), *Griffithsia globifera* ((144) p. 646), and *Spermothamnion Turneri* ((53) p. 568), but most investigators describe it as lying freely in the cytoplasm (fig. 141 K). Yamanouchi records centrosomes in *Polysiphonia* (fig. 141 D, *ce*) and *Corallina*, and they have also been reported in *Laurencia*, but for the most part such structures have not been seen during mitosis in Red Algae. The nucleolus disappears as the chromosomes become aggregated on the equatorial plate (fig. 141 E, K) and is reconstituted in each daughter-nucleus.

Most authorities deny any participation of the nucleolus in the development of the chromosomes, but in *Nemalion* ((30) pp. 327, 341, (259) p. 621), *Griffithsia* ((144) p. 646) and *Dumontia* ((54) p. 453) so-called carysome-nuclei are recorded and the chromatin is stated to pass out of the nucleolus at the commencement of mitosis; Kylin ((123) p. 101) attributes this to poor fixation. The peculiar resting nuclei described by Mathias (157) in certain Ceramiaceae have not been observed by other investigators and are probably to be attributed to the same defect (cf. (255), (257) p. 572).

The resting nuclei of Bangiales ((41) p. 199) and of the less specialised Nemalionales (*Batrachospermum*, *Lemanea*, *Nemalion*, (124) p. 258, (126) p. 156, (128) p. 8) contain a large nucleolus but, apart from that, appear almost devoid of structure. The spindles in *Nemalion* are stated to be intranuclear, which is denied by Kylin, while Wolfe (259) records centrosomes. The nuclei of *Scinaia* and *Bonnemaisonia* ((124*a*) p. 549) appear to resemble those of the more specialised Florideae.

The General Features of Reproduction

Sexual reproduction in Rhodophyceae is invariably oogamous. The female organ (carpogonium, fig. 221), which usually bears a special receptive process (trichogyne), exhibits retention of the single ovum and the latter shows no contraction either before or after fertilisation. The male organ (antheridium) produces a single motionless male cell (spermatium, fig. 222) which is conveyed passively to the trichogyne. The zygote, either by direct division as in Bangiales or after the production of filamentous outgrowths (gonimoblasts) as in Nemalionales, gives rise to a number of sporangia, each forming a single naked spore (carpospore). In most Florideae, however, the gonimoblasts do not arise directly from the zygote, but from other cells (auxiliary cells) which either belong to the same branch-system as the carpogonium (fig. 224 E, F, *a*) or are more or less widely separated from it (fig. 224 G, *a*). Intimate combinations of carpogonia and auxiliary cells are termed procarps, and in them there is direct fusion between the carpogonium and the auxiliary cells, while when the latter are spatially separated, the products of the zygote-nucleus are conveyed to them by special connecting filaments (fig. 224 G, *co*), frequently

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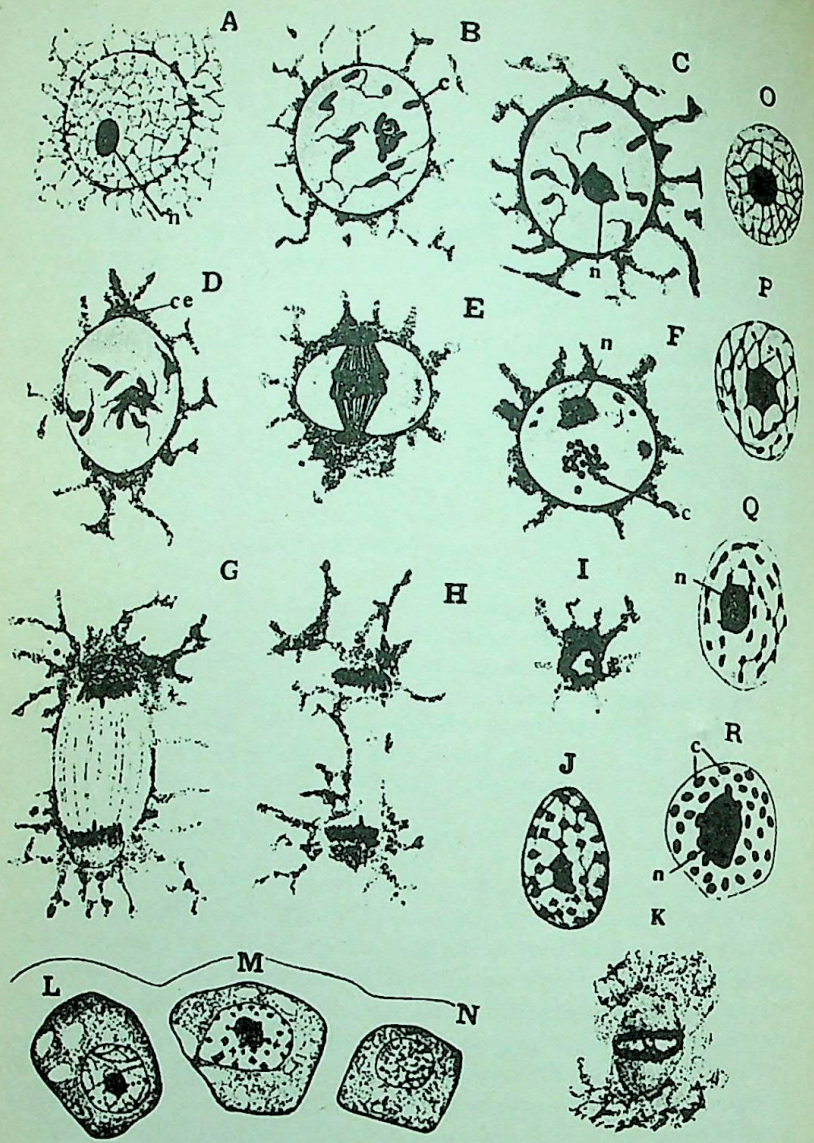

Fig. 141. Nucleus and vegetative nuclear division. A–I, *Polysiphonia violacea* (Roth) Grev. (after Yamanouchi), germinating tetraspore; A, resting nucleus; B, C, two sections of same nucleus in early prophase; D, late prophase, with centrosomes; E, metaphase; F, polar view of equatorial plate, 20 chromosomes and remains of nucleolus; G, anaphase; H, late anaphase, original nuclear membrane entirely dissolved; I, polar view at late anaphase. J–N, *Delesseria sanguinea* (L.) Lamour. (after Svedelius); J, late prophase of tetrasporic plant; K, anaphase; L–N, margin of frond of a tetrasporic plant, showing nuclei in different stages of prophase. O–R, *Rhodomela virgata* Kjellm. (after Kylin), prophase stages from a tetrasporic plant. *c*, chromosomes; *ce*, centrosomes; *n*, nucleolus.

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elongate and usually several in number. A descendant by division of the zygote-nucleus passes into the auxiliary cell and, after degeneration of its nucleus, gonimoblasts producing carpospores arise from the auxiliary cell. In many Florideae there is a marked fusion of cells during the development of the gonimoblast, a process connected with the supply of nutriment to the maturing carpospores.

Reduction occurs either at the first divisions of the zygote-nucleus (Bangiales, Nemalionales) or it is postponed and takes place in special tetrasporangia, borne on individuals distinct from, but morphologically identical with, the sexual plants (other Florideae). In Bangiales and Nemalionales there are thus two haploid phases (the sexual individual, the carpospore-bearing stage) and the life-cycle is haplobiontic; in the remaining Rhodophyceae there are two diploid phases (the carpospore-bearing stage, the tetrasporangiate individual) and the life-cycle is diplobiontic. With few exceptions the tetrasporangia form four spores which exhibit three types of arrangement within the sporangium (cruciate, zonate, tetrahedral, fig. 225). Direct reproduction of the sexual phase by means of accessory spores (usually monospores) is met with especially in Bangiales and Nemalionales. The reproductive features of Florideae are discussed in full on p. 591 et seq.

Classification and Status of the Rhodophyceae

The Rhodophyceae are at present grouped in seven orders (cf. (130) p. 113, (131) p. 90, (181) p. 378),[1] six of which belong to the Florideae. These orders are mainly distinguished by details of reproduction, although vegetative features are commonly also of significance. This will be evident from the following brief epitome:

A. Bangioideae. Simple forms with diffuse growth, never exhibiting aggregation of filaments and devoid of pit-connections; sex organs little specialised; carposporangia formed by direct division of the zygote. Terrestrial, freshwater, and marine. Only order

I. *Bangiales.* Unicellular, colonial, filamentous, or parenchymatous forms, commonly with a single axile, stellate chromatophore in the cells; haplobiontic; accessory reproduction by monospores.

B. Florideae. Filamentous forms, usually exhibiting aggregation of one or more branched filamentous axes to form compact pseudoparenchymatous thalli; pit-connections invariably present between the cells; sex organs highly differentiated; carposporangia formed on filamentous gonimoblasts derived directly or indirectly from the zygote. Largely marine.

[1] The order Nemastomales at first distinguished by Kylin was subsequently merged in the Gigartinales (133). No essential contribution is made by Wilke (258).

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II. *Nemalionales*. Heterotrichous, with uni- or multiaxial construction, cells commonly with a single chromatophore; haplobiontic; gonimoblasts usually arising from the carpogonium; accessory reproduction by monospores or tetraspores. Some fresh-water forms.

III. *Gelidiales*. Uniaxial; probably diplobiontic, but without auxiliary cells; compound procarp (see p. 628); tetrasporangia usually cruciate.

IV. *Cryptonemiales*. Uni- or multiaxial, with evident or indistinct heterotrichy in the young stages; diplobiontic; auxiliary cells sometimes remote from the carpogonia, both borne on accessory laterals which are sometimes aggregated into special fertile tracts (nemathecia, conceptacles); tetraspores cruciate or zonate.

V. *Gigartinales*. Uni- or multiaxial, heterotrichy of juvenile stages often indistinct; diplobiontic; procarps frequent, with auxiliary cells commonly lodged in the carpogonial branches which are borne on the ordinary laterals of the thallus; tetraspores cruciate or zonate.

VI. *Rhodymeniales*. Multiaxial, heterotrichy obscure; diplobiontic, with a definite procarp; auxiliary cells not specially differentiated until after fertilisation; tetraspores cruciate or tetrahedral.

VII. *Ceramiales*. Uniaxial, without heterotrichy; diplobiontic; procarp with 4-celled carpogonial branch, always borne on a pericentral cell from which the auxiliary cell is cut off only after fertilisation; tetraspores usually tetrahedral.

The Rhodophyceae afford no evidence of relationship to any other class of the Algae. Some have sought an affinity with the Myxophyceae (cf. (31) pp. 28, 36, (156) p. 16, (226) p. 14, (227) p. 670, (243)) owing to the presence of similar pigments (cf. however (22) p. 102), the absence of motile reproductive cells, and the occurrence in certain Blue-green Algae of cytoplasmic connections. Such a view overlooks entirely, quite apart from essential differences in metabolism, the barrier constituted by the fundamental contrast in cell-structure between the members of the two classes and by the absence of any type of sexual reproduction in Myxophyceae. There is no evidence that the type of cellular organisation found in the latter has ever evolved into that characteristic of most other plants ((68) p. 237). Those who uphold the view of an affinity with Blue-green Algae look especially to the Bangiales, but here the contrasts are just as patent (cf. p. 437). As little can be said in favour of a relationship between Bangiales and the Prasiolaceae among Chlorophyceae.

There is a considerable resemblance (cf. 1, p. 284), both in the female organ and in the general nature of the life-cycle, between *Coleochaete* and the haplobiontic Red Algae ((215) p. 250), but the differences are far too significant to admit of any question of affinity. Several authorities ((45), (50), (74) p. 248, (180) p. 137, (215) p. 243) have discussed the question of a relationship with Ascomycetes, the

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Laboulbeniales in particular being regarded as presenting points of contact. I am not sufficiently familiar with these groups, nor is a detailed discussion feasible, but such resemblances as have been emphasised appear to me to be more of the nature of parallel developments and not to afford evidence of any phylogenetic connection.

Literature relating to the Introductory Discussion of Rhodophyceae

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See No. 261 on p. 49 (Lunde & Lie, 1938). **266.** See No. 263 on p. 49 (Norris, Simeon & Williams, 1937). **267.** See No. 236 on p. 48 (Tammes, 1900). **268.** See No. 79 on p. 749 (Bruns, 1894). **269.** FOURMENT, R. & J. 'Sur l'utilisation du *Pterocladia capillacea* (Gmel.) Born. et Thur. Floridée, Gelidiacée dans la préparation de milieux solides, etc.' *Bull. Soc. Hist. Nat. Afrique du Nord*, 32, 176–80, 1941. For further references, see p. 898.

Sub-class I. BANGIOIDEAE

Order *BANGIALES*

Most of the Bangiales are probably annuals which enjoy a wide distribution over the surface of the earth. They exhibit practically all the simpler types of plant-body, although the latter never reaches any high degree of elaboration. One series of forms, with a filamentous or foliose thallus (Bangiaceae), are essentially marine, while another series (Porphyridiaceae), consisting for the most part at least of reduced forms, are more frequently met with in freshwater or terrestrial habitats. Some such classification has been advocated by most recent authorities ((78) p. 39, (103) p. 56, (118) p. 193; cf. also (141)), and the vegetative structure of the two families will best be discussed separately.

The thallus of most Bangiales lacks a definite growing point and exhibits diffuse growth. Adjacent cells are never connected by pits. There is typically a single axile, massive chromatophore, more or less stellate in shape and including a conspicuous central pyrenoid (fig. 143 B, P, R). The products of photosynthesis accumulate near the chromatophores as solid granules, resembling Floridean starch (132), and the varied pigmentation of the cells (91) is due to a form of phycoerythrin and to phycocyanin. The membranes probably consist largely of pectic substances (140); cellulose has been demonstrated only in *Porphyridium* (37), and *Erythrotrichia* ((74) p. 420). The nucleus (fig. 143 C, I, T, *n*) is often excentric in position.

VEGETATIVE STRUCTURE

(i) BANGIACEAE ((8), (9), (47), (60), (80), (103) p. 55, (108), (110))

The least specialised members of this family are those grouped as Erythrotrichieae. *Erythrotrichia* ((1) p. 14, (30) p. 146) comprises a number of small marine epiphytes, in several of which (e.g. *E. Boryana* (Mont.) Berth. (*Porphyra Boryana* Mont. (136) pl. 8A), *E. obscura*, fig. 142 J) the plant has the form of a heterotrichous filament, the one-layered discoid base (*d*), produced first by the germinating spore, bearing several, usually unbranched, erect threads (*e*). The degree of development of the disc varies, but in certain individuals it is the only part present and gives rise to the spores.[1] In

[1] Schmitz ((110) p. 313; cf. also (6) p. 376) founded the genus *Erythropeltis* for *Erythrotrichia discigera* Berth. in which such reduction often occurs. It may be doubted whether there is a basis for generic distinction (cf. (11) p. 9, (30) p. 146, (39), (47) p. 283, (55) p. 80). Kylin ((78) p. 45) advocates the retention of *Erythropeltis* for the heterotrichous species of *Erythrotrichia*.

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other species, however, the filaments are merely attached by an irregularly lobed basal cell (fig. 142 L), supplemented by short radiating rhizoids (*r*); this is so in *E. carnea* and *E. ceramicola* Aresch. (*Bangia ceramicola* Chauv. (53) pl. 317), the latter often regarded as a synonym of the former. The erect filaments may remain uniseriate (*E. ceramicola*), but in certain species (e.g. *E. obscura*, cf. (9) p. 26, (12) p. 8) all except the basal cells become divided by longitudinal, often followed by transverse, walls so that the threads assume a characteristic clavate form (fig. 142 J, K).

The freshwater *Kyliniella* (113), likewise with a heterotrichous habit (fig. 142 G), is distinguished by the possession of a parietal chromatophore devoid of a pyrenoid. The elongate erect threads, which are surrounded by a wide mucilage-envelope, produce only rhizoid-like branches by means of which they attach themselves to adjacent plants; they can form secondary discs at their tips.

Erythrocladia ((11) p. 7, (34) p. 798, (56) p. 112, (103) p. 71), a completely prostrate epiphyte or endophyte, forms small discs composed of a radiating system of threads in which the marginal cells are often bifid (fig. 142 B–D); in some species the discs are several-layered. This genus affords an interesting parallel to similar prostrate types among Chaetophorales. The chromatophore (*c*) is a lobed parietal plate with a pyrenoid.

A related form is perhaps constituted by *Colaconema*[1] ((5) p. 8), the species of which are endophytic in the membranes of various Algae (cf. (18) p. 180, (21-23), (120) p. 237). The cells of the irregularly branched filaments, which sometimes anastomose, contain parietal plate-shaped chromatophores. Although the genus has been placed near *Acrochaetium* ((7) p. 57, (24) p. 300, (48) p. 89), Rosenvinge ((103) p. 71), as well as Howe and Hoyt ((56) p. 113), draw attention to the resemblance to *Erythrocladia*, and further investigation must show whether the two genera are possibly but different developments of the same generic type.

Another form with a parietal, markedly lobed chromatophore is *Porphyropsis coccinea*[2] ((103) p. 68) which occurs as small one-layered *Porphyra*-like sheets (fig. 144 D). The young stages (fig. 144 E) form several-layered cushions, which become vesicular through active division of the upper layer; later the vesicle breaks open and constitutes a monostromatic frond which is at first cup-shaped (cf. *Monostroma*, *Omphalophyllum*). Subsequently numerous rhizoids arise from the lower cells.

The Bangieae, comprising *Bangia* and *Porphyra*, show greater specialisation. The unbranched threads of the former ((1) p. 16, (31), (98), (103) p. 56) may for a time (fig. 142 E) remain uniseriate, but the

[1] Schmitz ((110) p. 452) founded a genus of Rhodomelaceae (cf. also (33) p. 531) under the name *Colaconema*. This has been renamed *Colacopsis* by De Toni ((124) p. 1170).

[2] *Porphyra coccinea* J. Ag. Kuckuck ((70) p. 390) already expressed doubts about the reference of this species to *Porphyra*.

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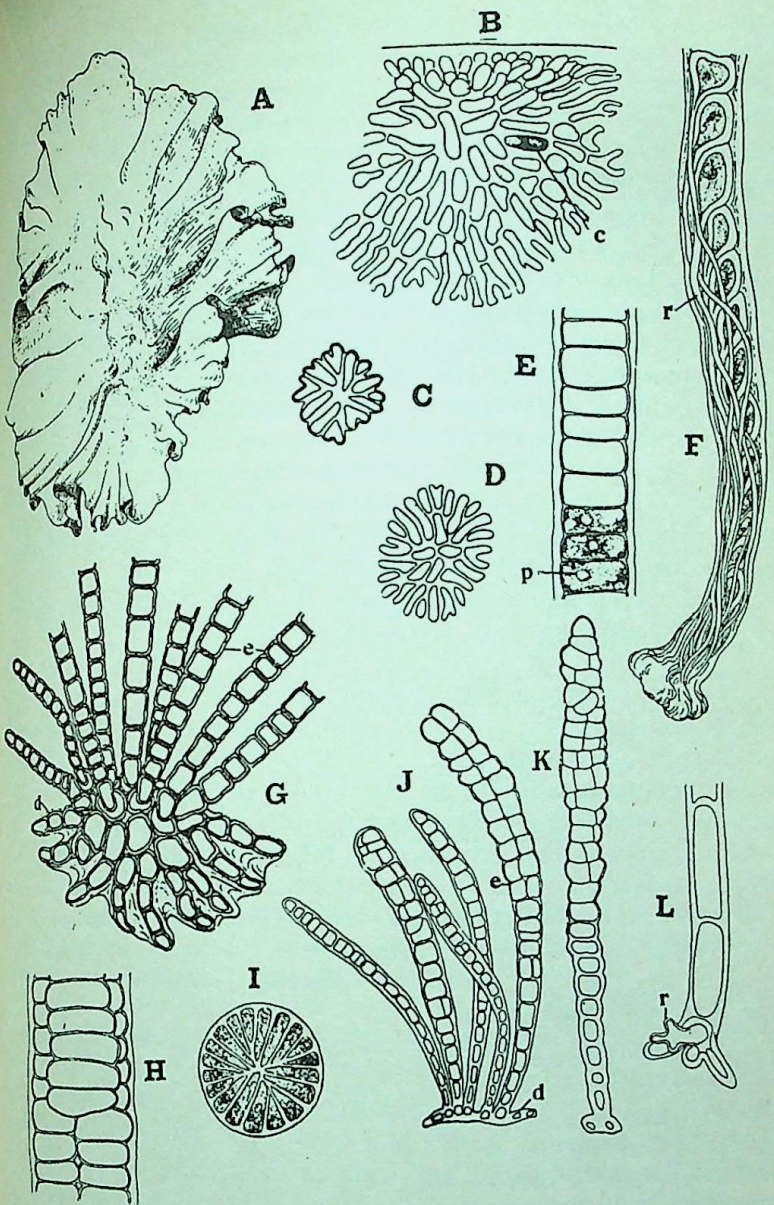

Fig. 142. A, *Porphyra umbilicalis* (L.) J. Ag., habit. B–D, *Erythrocladia subintegra* Rosenv.; C, D, stages in development of the disc. E, F, H, *Bangia fusco-purpurea* (Dillw.) Lyngb.; E, part of a young thread; F, base of an older thread, showing rhizoid-formation; H, part of mature thread. G, *Kyliniella latvica* Skuja. I, *Bangia atro-purpurea* (Roth) Ag., transverse section of mature thread. J–L, *Erythrotrichia*; J, K, *E. obscura* Berth., two plants; L, *E. carnea* (Dillw.) J. Ag., base of a thread. *c*, chromatophore; *d*, prostrate and *e*, erect systems; *p*, pyrenoid; *r*, rhizoid. (B after Rosenvinge; C, D after Kylin; G after Skuja; I after Reinke; J, K after Boergesen; the rest after Taylor.)

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older cells soon undergo longitudinal division (fig. 142 H) by approximately radial walls so that the circular cross-section exhibits fifteen or more sectors (fig. 142 I); occasional cells may remain undivided. Reinke ((98) p. 276) refers to a dome-shaped apical cell, but later workers make no mention of this and there is certainly abundant intercalary division. The young threads are merely attached by the basal cell, but in older plants the lower cells produce non-septate rhizoids (fig. 142 F, *r*) which grow through the thick gelatinous wall and spread out over the substratum.

B. atropurpurea is a characteristic inhabitant of the estuarine parts of rivers, where it forms dark-coloured (brown, violet, or almost black) tufts, the individual threads being up to 6 cm. long and as much as 200 μ wide; it is also reported from Lake Balaton (107). Woloszynska (133) describes band-shaped thalli, often encrusted with lime. The marine *B. fusco-purpurea* ((53) pl. 96), with equally broad but longer filaments (10–15 cm.), occurs near high water mark, sometimes in the spray zone, and is found especially in winter and spring; it has a marked capacity to withstand desiccation ((9) p. 7, (35) p. 185) and changes in salt-concentration (127, 128). Its dense, dark red or brownish-violet tufts are commonly associated with species of *Urospora*.

Porphyra ((1) p. 38, (9), (57), (58), (60) p. 241, (102) p. 826, (122) p. 59, (132)) is also usually at first a simple filament ((103) p. 64, (122) p. 59) which is stated ((9) p. 3, (69)) to grow for some time by means of an often three-sided apical cell. The abundant longitudinal division, which soon spreads from near the tip backwards, leads to the formation of a usually one-layered expanse of varying width (fig. 142 A) which exhibits diffuse growth. The cells are elongated perpendicular to the surface (fig. 144 O) and possess strongly thickened external walls covered by a "cuticle" (*cu*). The spores of *P. naiadum* produce a prostrate several-layered cushion from which the upright fronds arise ((57) p. 180, (68)), the only instance in which a *Porphyra* retains the heterotrichous condition.

The attaching system is constituted by thick-walled spreading rhizoids, produced on both surfaces from the lower cells of the thallus (cf. also (45)) and usually interweaving to form a compact cushion from which accessory fronds may later arise. The rhizoids are unicellular but multinucleate and some are branched; their dilated tips can divide into a number of cells. They adhere to the substratum by means of their gelatinous walls, as well as by suckers arising on their lower sides. Grubb ((45) p. 139) records penetration of the rhizoids to considerable depths into the tissues of *Fucus*. In some species the lower parts of the thalli are possibly perennial ((9) p. 20).

The species of *Porphyra* mainly inhabit the rocks between tide-levels and a number, which show marked resistance to desiccation ((35) p. 189, (88)), form characteristic zones at certain times of the year in the upper

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littoral region (cf. e.g. (46), (64) p. 11, (73) p. 3). The broad thalli are often unbranched and commonly have a wavy margin (fig. 142 A), as in *P. umbilicalis* (*P. vulgaris* Ag. (53) pl. 211) which reaches a length of 30 cm. The narrow *P. linearis* Grev. ((53) pl. 2), usually regarded as a growth-form of *P. umbilicalis* ((25) p. 29, (45) p. 132, (96); cf. however (20) p. 58, (36) p. 250, (99)), is found mainly in winter and frequently forms a belt above that occupied by the latter. Other common species are *P. atropurpurea* (Olivi) De Toni (*P. leucosticta* Thur.) and *P. perforata* J. Ag., the latter abundant on the Pacific coasts of North America. Many species are or have been used as food, for instance the "laver" of Wales and Scotland which is derived from *P. umbilicalis* and *P. laciniata*. In Japan species of *Porphyra* are specially cultivated, being grown on prepared twigs which are exposed during winter ((65) p. 22, (134)); "Nori" is dried *P. tenera*.

(ii) Porphyridiaceae

Apart from *Goniotrichum* (fig. 143 A) and *Asterocytis* (fig. 143 E), with branched or unbranched filaments, the Porphyridiaceae include several, probably reduced, unicellular and mainly terrestrial types, the cells of which are commonly aggregated to form brightly coloured masses. The commonest, *Porphyridium cruentum*, is not infrequent on soil and on damp walls, where it forms several-layered blood-red mucilaginous strata (fig. 143 H), although when dry the brittle crusts are less conspicuous. In *Porphyridium* (fig. 143 D) the individual cells are globose, whereas in *Chroothece* (fig. 143 T, V) they are ellipsoidal. The reference of these diverse forms to Bangiales depends largely on the possession of axile star-shaped chromatophores and the presence of Floridean starch.

The species of *Goniotrichum* ((1) p. 11, (9) p. 26, (11) p. 4, (103) p. 75) are minute epiphytes, usually with plentifully branched filaments (fig. 143 A), possessing thick longitudinal walls (fig. 143 B, F, J). The branching is often described as false and like that of certain Myxophyceae, the upper part of the parent-thread being pushed aside by the outgrowth of the part below (cf. fig. 143 B, J), but this requires further investigation ((24) p. 230, (85) p. 276). In *G. elegans*[1] the threads commonly remain uniseriate (fig. 143 B, J), but in *G. cornu cervi* (Reinsch) Hauck (*G. dichotomum* Berth. (47) p. 450), *G. Humphreyi* Collins ((11) pp. 10, 445), and others eight or more rather irregularly arranged cells may be seen in the transverse section (cf. fig. 143 F). The older cells appear rounded or discoid; all are capable of division. In the little-known *Neevea* ((6) p. 373) the branched, uni- or multiseriate threads form sheets which are endophytic in *Flustra*.

Phragmonema ((41) p. 373, (137) p. 49), so far only found on leaves and walls in hothouses, is distinguished by the presence of several parietal band-shaped chromatophores in each cell (fig. 143 K–M, *c*). The rarely

[1] *Bangia elegans* Chauv. ((53) pl. 246). According to some the species is more correctly named *G. Alsidii* (Zanard.) Howe ((56*a*) p. 553).

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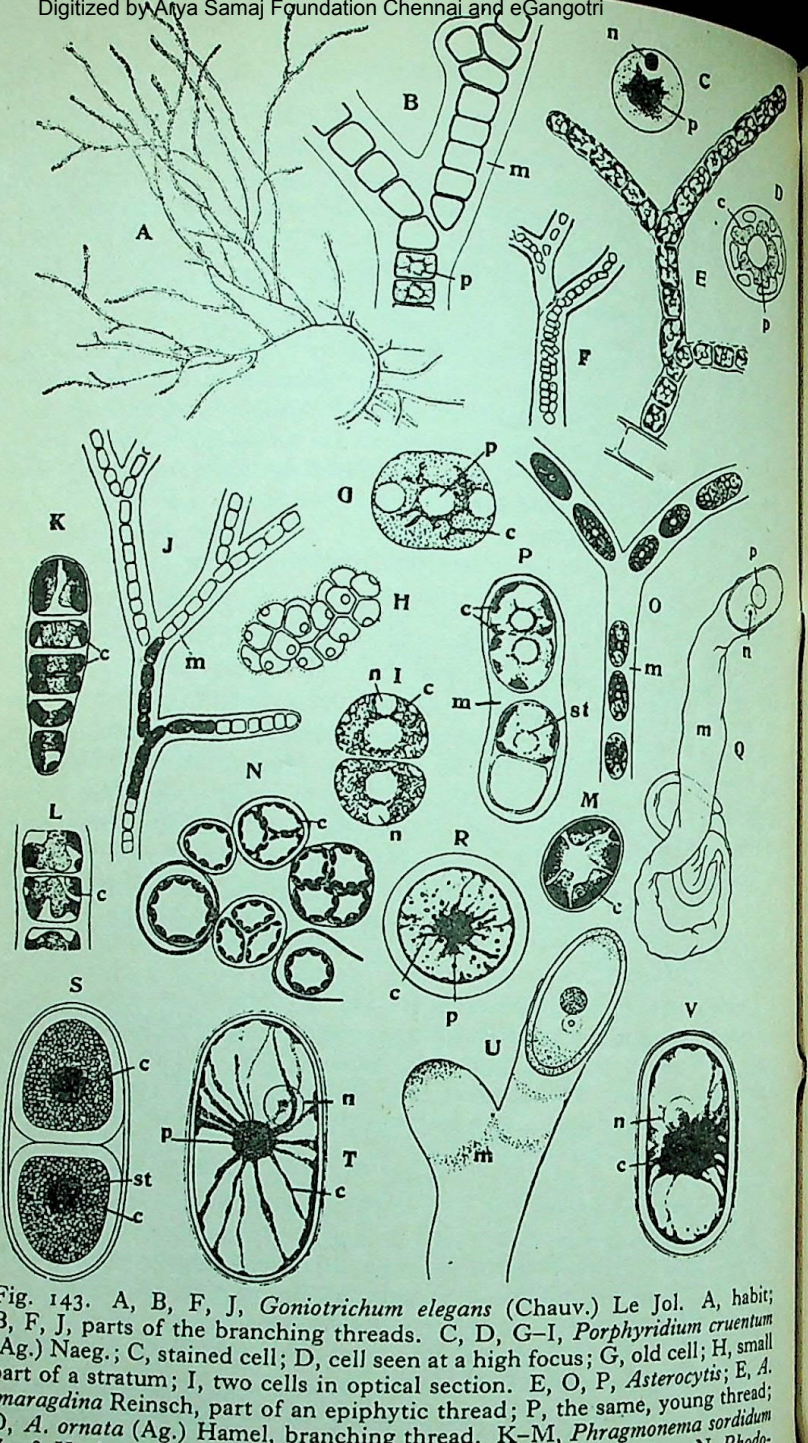

Fig. 143. A, B, F, J, *Goniotrichum elegans* (Chauv.) Le Jol. A, habit; B, F, J, parts of the branching threads. C, D, G–I, *Porphyridium cruentum* (Ag.) Naeg.; C, stained cell; D, cell seen at a high focus; G, old cell; H, small part of a stratum; I, two cells in optical section. E, O, P, *Asterocytis*; E, *A. smaragdina* Reinsch, part of an epiphytic thread; P, the same, young thread; O, *A. ornata* (Ag.) Hamel, branching thread. K–M, *Phragmonema sordidum* Zopf; K, short thread; L, piece of same; M, cell in optical section. N, *Rhodospora sordida* Geitler, small part of a stratum. Q–V, *Chroothece mobilis* Pascher & Petrova; Q, U, formation of mucilage-strands; R, T, V, cells from cultures, in R in cross-section; S, cells from nature. *c*, chromatophores; *m*, mucilage; *n*, nuclei; *p*, pyrenoids; *st*, starch. (A, B after Taylor; F, J after Rosenvinge; Q–V after Pascher & Petrová; the rest after Geitler.)

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branched threads are of a dull violet or olive colour and exhibit ready fragmentation into single cells.

The dense tufts formed by *Asterocytis ornata*[1] (*A. ramosa* (Thw.) Gobi; *Hormospora ramosa* Thw. (53) pl. 213; *Goniotrichum ramosum* Hauck) consist of branched or unbranched tubular strands of mucilage containing variously shaped (commonly ellipsoidal) cells arranged in a single row (fig. 143 O); the blue-green chromatophore is often excentric. This species is widespread in brackish water, and appears to be rather indifferent to the salt concentration; it is probably an eutrophic form ((83) p. 71, (112) p. 17). *A. halophila* (Hansg.) Forti is also recorded from freshwater.[2] A brackish water form, frequently referred to this genus, is *Allogonium smaragdinum* Hansg. ((41) p. 367, (52) p. 132, (115) p. 121), which occurs as short, rarely branched, threads (fig. 143 E) or commonly as single cells. In nature the older cells are often filled with starch and almost colourless, but in well-nourished individuals the radiating processes of the chromatophores, commonly dilated at their ends, become prominent (fig. 143 E, P). The cells can escape from the mucilage-envelope and perform slow tortuous movements (101); a mechanism similar to that of *Chroothece* is suspected. Pascher, in fact, regards *Asterocytis* as a colonial development of the latter genus.

Chroothece Richterianum Hansg. ((49) p. 353, (51) p. 104), occurring as orange- to brownish-yellow mucilage-masses on saline soils in Bohemia, is little known, but Pascher and Petrová (93) have described in greater detail a second species (*C. mobilis*), which forms greyish-yellow mucilage-masses on moorland soils. In both species the ellipsoidal cells (fig. 143 T, V) possess a thick stratified pectic membrane. In nature those of *C. mobilis* for the most part occur in a resting condition (fig. 143 S) in which the cells are filled with starch (*st*) and only the axile part of the chromatophore (*c*) persists, but if kept in the dark the starch vanishes and the stellate-blue-green chromatophore becomes apparent (fig. 143 T, V, *c*). The cells multiply by transverse division into two (fig. 143 S) or four daughter-cells which secrete distinct membranes, but remain for a time enclosed in that of the parent, as a result of which temporary threads may be formed. The pyrenoid either divides with the protoplast or, more generally, a new pyrenoid is formed in one of the daughter-cells, the chromatophore gradually differentiating around it. Rejuvenescence of the cells is frequent.

When stained with fuchsin, a mucilage-strand (fig. 143 Q, *m*), with occasional denser layers and as much as 50 times the length of the cell, becomes recognisable in *C. mobilis*; a similar, but more markedly stratified strand is recorded in *C. Richterianum*. In *C. mobilis* the mucilage is no doubt secreted through the numerous pores which traverse the membranes and are specially abundant towards the poles (fig. 143 U). The nucleus is commonly situated at that end of the cell from which

[1] See (12) p. 11, (47) p. 451, (94) p. 159, (103) p. 77, (109) p. 717, (131) p. 7; cf. also *A. Wolleana* (Hansg.) Lagerh. (*Chroodactylon Wolleanum* Hansg. (50)), which may be a form of *A. ornata* (32).

[2] The freshwater members of *Asterocytis* require further study. There is possibly confusion with similar Myxophyceae ((130) p. 432).

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active secretion is occurring. The formation of these strands is doubtless related to the rapid jerky, often zigzag, movements which are exhibited by occasional cells and last but for a fraction of a second, during which a distance equal to ten times the length of the cell may be covered (cf. Desmids). Rise of temperature increases the frequency of the movement which is ascribed to rapid absorption of water on the part of the mucilage.

The spherical cells composing the crusts of *Porphyridium cruentum*[1] are provided with individual mucilage-envelopes and embedded in a common mass of hyaline mucilage; at times they develop mucilage-stalks which are sometimes branched ((126) p. 71). The cells multiply by simple division in various directions. There is some difference of opinion as to the cell-structure; Staehelin's (116) data are certainly in large part erroneous ((17) p. 457). The cell-wall is thin and elastic (fig. 143 D, G, I) and follows all changes in the volume of the protoplast ((16) p. 541). The body of the chromatophore, the red coloration of which is due to phycoerythrin ((37), (38), (86) p. 811), is very massive, while the radiating processes are often short (fig. 143 D, I) or ((43) p. 601) completely lacking. The peripheral cytoplasm between the processes of the chromatophore includes many small vacuoles. The relatively large nucleus, which appears as a white area in the living cell, lies adpressed to the wall (fig. 143 I, *n*); when stained it shows a nucleolus and an outer nucleus devoid of chromatin ((41) p. 366). The mitotic stages described by Lewis and Zirkle ((84) p. 338) are, according to Geitler, misinterpretations. Both starch and fat may be present ((126) p. 74).

In recent years a number of other species, all with essentially the same structure, have been described. *P. aerugineum* Geitler ((40), (41) p. 362), which is stated to be widely distributed in stagnant freshwaters (42) and has also been found on soil (139), lacks phycoerythrin and owes its blue-green colour to the presence of phycocyanin. Kylin (77) has recorded a marine species, at present only known in cultures (*P. marinum*).

Rhodospora (42) possesses cells with a central nucleus and numerous parietal discoid chromatophores (fig. 143 N). It forms indefinite masses of a red-violet or dull olive-green colour on archaic rocks. The cells multiply by division along three planes into 2–16 (usually 4–8) parts which are liberated by the rupture of the parent-membrane (fig. 143 N).

REPRODUCTION OF BANGIALES

The only known method of multiplication in certain Porphyridiaceae (*Rhodospora*, *Chroothece*, etc.) is by cell-division (autospore-formation). Most Bangiales, however, exhibit asexual reproduction by structures variously called monospores ((110) p. 309), neutral spores

[1] See (15), (37), (41) p. 364, (71), (84), (110) p. 315, (115) p. 125, (126). Brand ((16) p. 543) gives details as to mode of occurrence; Kufferath (71) and Vischer ((126) p. 99), who studied the alga in pure culture, state that it will not grow in darkness, even in the presence of glucose.

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((9) p. 9) or gonidia ((103) p. 55). The first designation appears as suitable as any other and is adopted here. The naked monospores are liberated through a well-defined aperture in the wall of the sporangium (fig. 144 A), the process taking place either gradually or suddenly ((9) p. 10, (26) p. 191).

The *monosporangia* of *Porphyra* are generally formed by crosswise division of the vegetative cells perpendicular to the surface so that the thallus remains one-layered. Those of *Bangia* ((9) p. 9, (31) p. 30, (98) p. 281) are usually produced by one or two radial divisions in the sectors, the process mostly commencing at the apex of a thread; they may, however, arise from an entire cell without division ((110) p. 311) or even from the cells of the young uniseriate threads ((75) p. 3).

Erythrotrichia (fig. 144 A, B; (9) p. 10, (103) p. 68), *Erythrocladia* (fig. 144 C; (103) p. 73), and *Porphyropsis* (fig. 144 D; (103) p. 71) possess more clearly differentiated monosporangia which are constituted by small cells (*m*) cut off by a curved wall, usually from the upper end of a vegetative cell, after accumulation of cytoplasm at the point where the sporangium is to be formed. In *Erythrotrichia*, after liberation of the spore, the part of the vegetative cell below enlarges and fills the cavity (fig. 144 A, the third cell from below) and further sporangia may be produced from these cells.

The monospores of *Colaconema* are formed from terminal or intercalary sporangia which may be cut off from a vegetative cell ((56) p. 113) and are sometimes detached as a whole (23). Those of *Goniotrichum* ((9) p. 27, (109) p. 718, (110) p. 314), of *Asterocytis* ((109) p. 717, (131) p. 8), and probably of *Porphyridium cruentum* ((126) p. 78) are constituted by the protoplasts of the ordinary cells which round off and escape from their envelopes; in *Goniotrichum* the process begins in the upper parts of the threads and, according to Chemin ((24) p. 231), is preceded by longitudinal division of the parent-cells. Thick-walled akinetes have also been recorded in *Asterocytis* ((56*a*) p. 554, (103) p. 78, (131) p. 9).

The monospores of *Bangia* and *Porphyra* show amoeboid changes of shape ((9) p. 11, (75) p. 4, (98) p. 282) which do not appear to be accompanied by any appreciable translocation. They commence some little time after liberation and may continue for two days. Such changes of shape are also recorded in *Porphyridium*. The monospores of *Erythrotrichia* and *Goniotrichum* do not appear to show this feature (cf. however (30) p. 147), although they exhibit gliding movements ((9) p. 11, (24) p. 226, (105) p. 73) which are sometimes quite rapid; similar movements have been observed in *Porphyridium* ((28), (43), (126) p. 78). The mechanism of the movement is unknown, but light sometimes appears to exert a directive influence ((9) p. 11).

Sexual reproduction is recorded only in *Bangia*, *Porphyra*, *Erythrotrichia* and *Erythrocladia*[1] and has so far not been observed

[1] Earlier accounts (69, 98) of the sexual process are erroneous. The details for *Erythrocladia* ((56) p. 112)) are unclear. The exserted spermatia recall the fertilisation-stages figured for other Bangiales.

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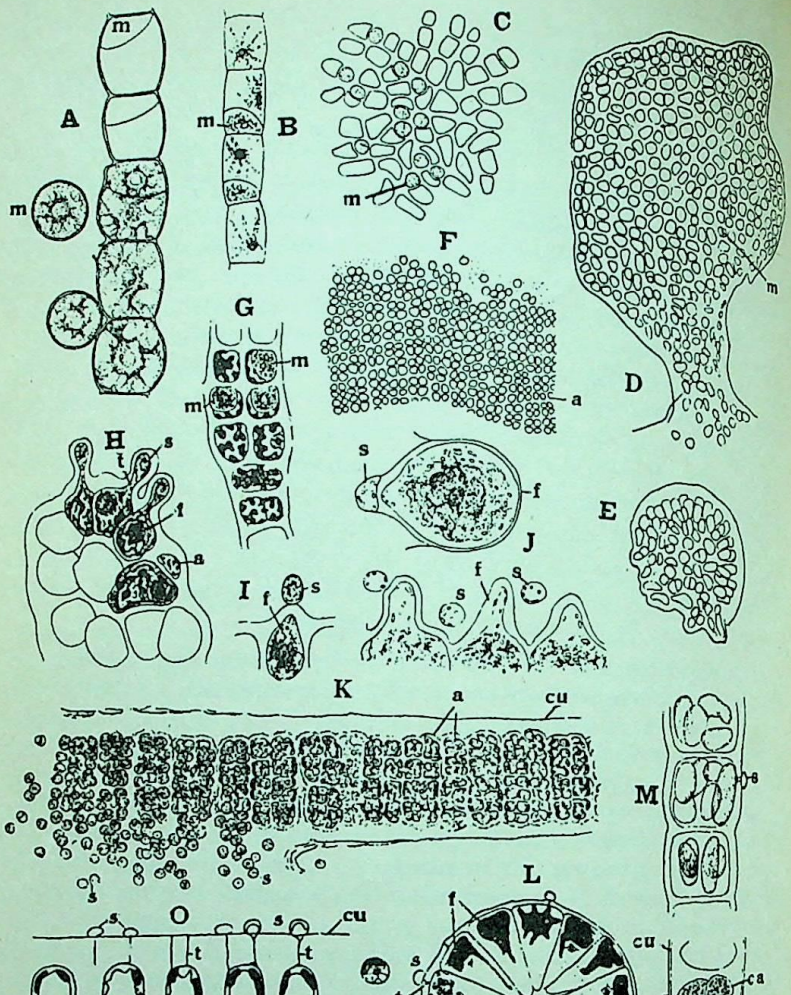

Fig. 144. A, B, G–I, *Erythrotrichia*; A, B, *E. carnea* (Dillw.) J. Ag., formation and liberation of monospores; G, *E. obscura* Berth., formation of monospores; H, I, the same, male and female sex organs and fertilisation. C, *Erythrocladia subintegra* Rosenv., monospore-formation. D, E, *Porphyropsis coccinea* (C. Ag.) Rosenv.; D, older thallus showing monospore-formation; E, young thallus. F, J, K, N, O, *Porphyra*; F, *P. umbilicalis* (L.) J. Ag., antheridia from the surface; J, *P. tenera* Kjellm., upper figure fertilisation, lower female organs and spermatia; K, *P. laciniata* (Lightf.) Ag., antheridial frond in

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in any freshwater member. As in Florideae, the male cells (spermatia) are devoid of organs of movement.[1] The distribution of the sexes is variable ((67) p. 207). In monoecious species of *Porphyra* they are commonly segregated, the male areas being yellowish-white or white, the female purple ((57) p. 188, (60), (103) p. 62); *P. tenera* is androdioecious ((72) p. 380). In the Bangieae sexual organs are often formed over a large part of the thallus, although growth may still continue in the lower parts after the apical ones have begun to form reproductive cells.

The antheridia of *Porphyra* ((26) p. 216, (46) p. 227, (58) p. 210, (60) p. 245, (82) p. 101, (122) p. 60) arise by repeated division of the cells (fig. 144 K). The first wall is parallel to the surface (cf. however, (57) p. 189) and the products undergo two vertical divisions; further horizontal walls lead to the formation of 32–128 small cells which are arranged in several layers. Antheridium-formation commences at the apex or edges and gradually spreads towards the base of the thallus. The antheridia of *Bangia* are produced in the same way, their formation often proceeding basipetally ((26) p. 187, (98) p. 275) and commonly involving the whole plant. The mature antheridia are colourless, but contain a small leucoplast ((9) p. 12, (26) pp. 200, 219, (58) p. 210, (60) p. 252). The spermatia (fig. 144 K, *s*) are liberated by gelatinisation of the membranes, although the boundaries of the original parent-cells long remain recognisable.

In *Erythrotrichia* ((9) p. 13) the antheridia are formed in the same way as the monosporangia. The spermatia are larger than those of Bangieae and have a more obvious plastid; they exhibit some capacity for movement. The correspondence between monospores and spermatia evident in this genus is also shown in *Porphyra atropurpurea* ((9) p. 13) where the same parent-cell may give rise both to monosporangia and antheridia; in such instances there are all transitions in size and colour between the two types of reproductive cells (cf. also p. 624).

The female organs (commonly called carpogonia) often differ from vegetative cells only in their somewhat larger size and more abundant contents (fig. 144 L, N, O, *f*). The surface is presumably always

[1] The motile gametes described by Yendo (135) are no doubt parasitic Fungi (75, 92).

section; N, *P. atropurpurea* (Olivi) De Toni, section, fertilisation and carpospore-formation; O, *P. umbilicalis* f. *linearis*, female organs in section and fertilisation. L, M, *Bangia*; L, *B. fusco-purpurea* (Dillw.) Lyngb., section, fertilisation; M, *B. pumila* Aresch., fertilisation. *a*, antheridia; *ca*, carposporangia; *cu*, cuticle; *f*, female cells; *m*, monosporangia or monospores; *s*, spermatia; *t*, connection between spermatium and carpogonium. (A, F, after Taylor; B after Boergesen; C, after Kylin; D, E after Rosenvinge; G-I, N after Berthold; J after Kunieda; K after Thuret & Bornet; L, O after Dangeard; M after Darbishire.)

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mucilaginous, since abundant spermatia (*s*), now enveloped by a thin membrane, are found adhering to them. In *Erythrotrichia* ((9) p. 17) and diverse species of *Porphyra* ((9) p. 14, (26) p. 212, (72) p. 388) the surface of the female organ is protruded (fig. 144 H–J, *f*), although it is not clear whether this is primary or secondary. It has repeatedly been recorded ((8) p. 81, (9) p. 15, (61) p. 145) that, if fertilisation be delayed, the female cells of *Porphyra* put forth on both surfaces elongate hyaline protuberances to which spermatia can adhere; less pronounced structures of the same type have been observed in *Bangia*. These outgrowths have been compared with trichogynes.

In the process of fertilisation[1] ((8), (9) p. 14, (26) pp. 202, 222, (58), (61) p. 144, (103) p. 63) the spermatium puts forth an often delicate process (fig. 144 H, L, N, O, *t*) containing a thin strand of cytoplasm. This penetrates rather rapidly through the thick membrane to the female protoplast (*f*), and the greater part of the contents of the spermatium (*s*) pass into the latter. Dangeard ((26) p. 202) observed the sexual nuclei in contact. The connecting strand of cytoplasm often persists for a long time, while the empty spermatium-wall at the surface soon disappears. Kunieda ((72) p. 389), who describes a rather different method of sexual fusion in *Porphyra tenera* (fig. 144 J), suggests that the stages previously described do not represent fertilisation, but are due to the attack of a parasite; no adequate evidence is produced for this view.

After fusion there is increase of cytoplasm and accumulation of starch in the female cell, while the chromatophore withdraws its processes and forms an irregular lobed mass. Rosenvinge ((103) p. 63) records the occurrence of groups of carpospores in *P. umbilicalis*, without any evidence of fertilisation-tubes, and suggests the possibility of an apogamous development.

In *Erythrotrichia* ((9) p. 17) the undivided female protoplast is set free after fertilisation. In the Bangieae, on the other hand, there is usually successive segmentation into eight[2] (rarely more) parts, from each of which a naked carpospore is liberated, although if the female cells are small, there may be fewer or no divisions ((47) p. 436, (61)). In *Bangia* the first wall is periclinal ((9) p. 16; anticlinal according to (26) p. 193), the later ones radial, while in *Porphyra* the first wall is parallel to the surface and each of the products divides into quadrants ((8) p. 80, (26) p. 215, (60) p. 243, (122) p. 60) so that the carposporangia normally lie in two layers (fig. 144 N). The mature sporangia possess gelatinous walls and their boundaries remain clearly visible after the escape of the carpospores (fig. 145 A, B). In *P. tenera* ((72) p. 391) the parts of the fronds containing the maturing carpospores become de-

[1] The stages described by Knox ((68) p. 129) are open to suspicion.

[2] Hence the name octospores used by Janczewski (60) and Goebel (44). The fusions between escaped carpospores and spermatia described by Reinke ((98) p. 276) are erroneous.

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tached, and the latter are stated to remain dormant throughout spring and summer.

The liberated carpospores, which are always naked, contain much starch and are usually not as large as the monospores, while their chromatophore is smaller and less lobed or diffuse ((72) p. 381). They exhibit slight amoeboid movements ((9) p. 17, (60) p. 244, (75) p. 6, (100)), but round off before forming a membrane.

THE LIFE-CYCLE OF BANGIALES

There is reason to believe that the Bangiales, like the less specialised Florideae, are haploid forms in which reduction takes place during the first divisions in the zygote; this has been demonstrated in *Porphyra* ((26) p. 223) with some degree of probability. Sexual plants occur mainly during the cold season of the year, whilst at other times the thalli often bear monosporangia only. There can be no doubt that these represent merely an accessory method of reproduction. Many Bangieae disappear altogether during the warm season (54, 72, 135).

The monospores of the Bangieae develop direct into new plants ((24) p. 228, (26) pp. 205, 225, (29), (75) p. 5) and may germinate within the sporangia ((98) p. 281). After formation of a membrane the spore elongates (fig. 145 C, D) and divides transversely (fig. 145 E), the one cell giving rise to a rhizoid (*r*), while the other segments to form the primary filament (fig. 145 G–K); other rhizoids soon develop from the lower cells.

The fate of the carpospores remains uncertain. According to Kunieda ((72) p. 386) those of *Porphyra tenera* remain dormant throughout the warm season and give rise to fresh crops of plants in the late autumn; the method of germination is stated not to differ essentially from that of the monospores (fig. 145 M), although the germlings have thicker walls and diffuse chromatophores. Earlier investigators ((9) p. 19, (29), (46) p. 229, (60) pp. 244, 249, (75) p. 6, (98) p. 278, (122) p. 61, (135) p. 81), studying the development of the carpospores of *Bangia* and *Porphyra* in cultures, concluded that they gave rise to branched filamentous stages (fig. 145 L, O-Q) from which supposed monospores were liberated (fig. 145 N). Kunieda (p. 391) states that such stages are pathological. Rees ((96), (97) p. 249), studying the life-cycle of *P. umbilicalis* in nature, however, finds that the carpospores produce short little-branched filaments lasting only for a few weeks and multiplying by means of monospores; ultimately these give rise to the *Porphyra*-thallus. Ueda ((125); cf. also (67) p. 206, (92)) also concluded that the Japanese *Porphyras* persisted through the summer as minute thalli reproducing by monospores.

It appears probable that, in the Northern Hemisphere at least, the ordinary thallus propagates both by monospores and by sexual means, one or other at times preponderating. While the monospores repro-

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duce the thallus direct, the carpospores give rise to a filamentous stage which lasts during the unfavourable period and ultimately reproduces the ordinary plant. In some regions the ordinary thalli are

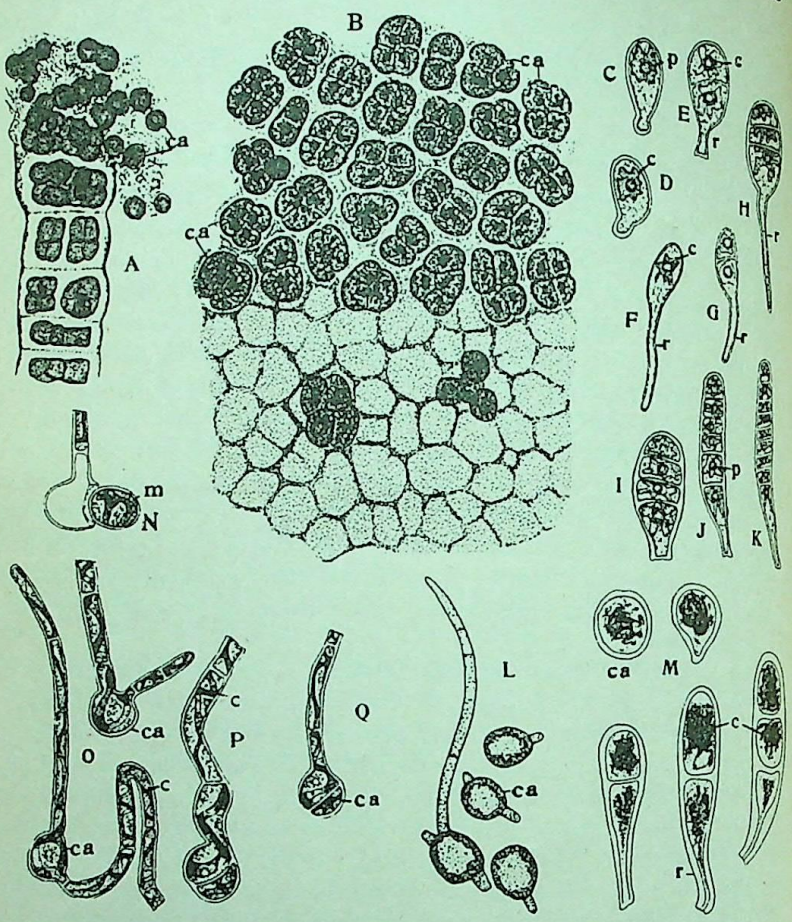

Fig. 145. A, C–L, *Bangia*; A, *B. pumila* Aresch., carpospore-development; C–K, *B. fusco-purpurea* (Dillw.) Lyngb., stages in germination of monospores; L, the same, germination of carpospores. B, N–Q, *Porphyra laciniata* (Lightf.) Ag.; B, surface-view of part of thallus with carpospores; N–Q, stages in germination of carpospores. M, *P. tenera* Kjellm., carpospore and four stages in germination. *c*, chromatophores; *ca*, carpospores; *p*, pyrenoids; *m*, monospore (?); *r*, rhizoids. (A after Darbishire; B after Thuret & Bornet; L after Reinke; M after Kunieda; the rest after Kylin.)

found throughout the year. The probable persistence by means of minute filamentous stages recalls the condition in many Ectocarpales (p. 132).

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THE AFFINITIES AND STATUS OF BANGIALES

Although certain authorities have advocated a relationship with Prasiolaceae (Ulotrichales; cf. (58), (81), (107*a*) p. 253, (108) pp. 229, 237, (111) p. 289) or Myxophyceae ((59), (79) p. 433, (123)), the bulk of opinion has always favoured an affinity with Florideae ((9) p. 21, (62), (76)). With Prasiolaceae there is nothing in common except the form of the thallus and chromatophore, while the Bangiales are fundamentally distinguished from the Myxophyceae by their cell-structure, the products of photosynthesis, and the methods of reproduction (cf. also p. 416). The simple nuclei described in *Porphyra tenera* by Ishikawa (58) depend on poor fixation; Dangeard ((26) pp. 198, 218, (27)) has shown that those of *Bangia* and *Porphyra* possess a nucleolus and undergo a mitotic division in which centrosomes are recognised. In view of the many important differences, the few resemblances cannot be taken as evidence of an affinity with Myxophyceae.

In discussing the relationship to Florideae, it may be noted that, apart from the simple vegetative structure, the absence of apical growth, and the lack of pits between the cells (p. 423), there are important contrasts in reproduction. Thus, the reproductive organs are formed from intercalary cells (76), the female organs are less specialised, and the entire zygote is used to form carpospores (cf. also (138)). Svedelius ((119) p. 228) does not regard the female organs as homologous with those of Florideae, since outgrowths resembling trichogynes are only sometimes present. Schmitz ((108) p. 235) also emphasised the differences in the method of fertilisation.

On the other hand, there are marked resemblances in the pigmentation of the chromatophores, in the presence of Floridean starch ((15) p. 415, (26) pp. 195, 218), in the general character of the spermatia and carpospores (especially their non-motility), and in the similarity between the life-cycle and that of Nemalionales. The chromatophores contain phycoerythrin and phycocyanin, as well as chlorophyll, carotene (142), and xanthophyll ((13) p. 193, (76)), and in *Porphyra tenera* the two first are stated (117) to be identical with those in *Ceramium rubrum*; the same is true of the phycoerythrin in *Porphyridium marinum* ((77) p. 3), although that of *P. cruentum* ((13) p. 191, (37), (86) p. 808) seems to be a different modification, resembling that found in Myxophyceae. Kylin (76) specially emphasises the identity of the pigments of Bangiales and Florideae and the contrast with Myxophyceae and other groups. In certain Porphyridiaceae the phycocyanin evidently predominates over phycoerythrin, and is perhaps alone present.

The physiological resemblances are probably significant, when taken in conjunction with the general parallel in reproductive methods. Rosenvinge (104) also lays stress on the similarity between the cell-

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structure of many Bangiales and diverse Nemalionales (p. 402); the two orders also resemble one another in the amoeboid movements exhibited by the spores. For these and other reasons he proposes the name Protoflorideae which I have hesitated to adopt, because it is doubtful whether the Bangiales can be regarded as precursors of the Florideae. The undoubted marks of relationship are more likely to be due to divergent development from a common ancestry. I am inclined to regard forms like *Erythrotrichia* and *Kyliniella* as the most primitive members of the group, despite the rather specialised monosporangia of the former, because in their heterotrichous habit they show the nearest approach to what was probably the prototype of Bangiales and Florideae.

The classification here adopted is as follows:

(*a*) *Bangiaceae*: Bangia, Colaconema (?), Erythrocladia, Erythrotrichia, Kyliniella, Porphyra, Porphyropsis.

(*b*) *Porphyridiaceae*: Allogonium, Asterocytis, Chroothece, Goniotrichum, Neevea, Phragmonema, Porphyridium, Rhodospora.

UNCERTAIN BANGIALES

Compsopogon[1] is chiefly a denizen of tropical and subtropical streams, although it has been recorded from ponds (19) and from tidal waters. Its occasional occurrence in temperate regions is no doubt due to introduction by shipping. Thus, *C. leptoclados* Mont. has been found in a part of the Reddish Canal, Manchester, where there is an influx of hot water from cotton mills ((129) p. 5). The rather coarse, richly branched threads are blue- or violet-green in colour. In the younger parts (fig. 146 A) they consist of flat cells formed by transverse division of the segments of the apical cell (*a*), but in the older parts the cells become greatly enlarged and barrel-shaped (fig. 146 B, *ax*); there are no pits. At some distance from the apex the axial cells cut off successive peripheral segments, which ultimately unite to form a compact cortex (*co*) of deeply pigmented cells through which the almost colourless axial ones are plainly visible. The cells of the cortex multiply by anticlinal division and sometimes divide to form 2–4 layers. No cortex is produced in the basal parts of the threads, where, however, the axial cells are commonly overgrown by septate rhizoids emanating from the lower cells ((121) p. 262). Branches arise before the cortex is formed (fig. 146 A), although short secondary branches may later originate from the cortical cells.

The cells contain numerous parietal oval to oblong chromatophores (fig. 146 C) which are sometimes lobed ((114) p. 605, (121) p. 261); the thread-like chromatophores drawn by Schmitz ((110) p. 319) have not been recorded by others. The cytoplasm of the axial cells shows circulation.

The only method of reproduction known is by monospores, of which Thaxter ((121) p. 263) distinguishes two kinds; both are spherical and

[1] See (2), (3), (87) p. 298, (110) p. 318, (114) p. 605, (115) p. 122, (121).

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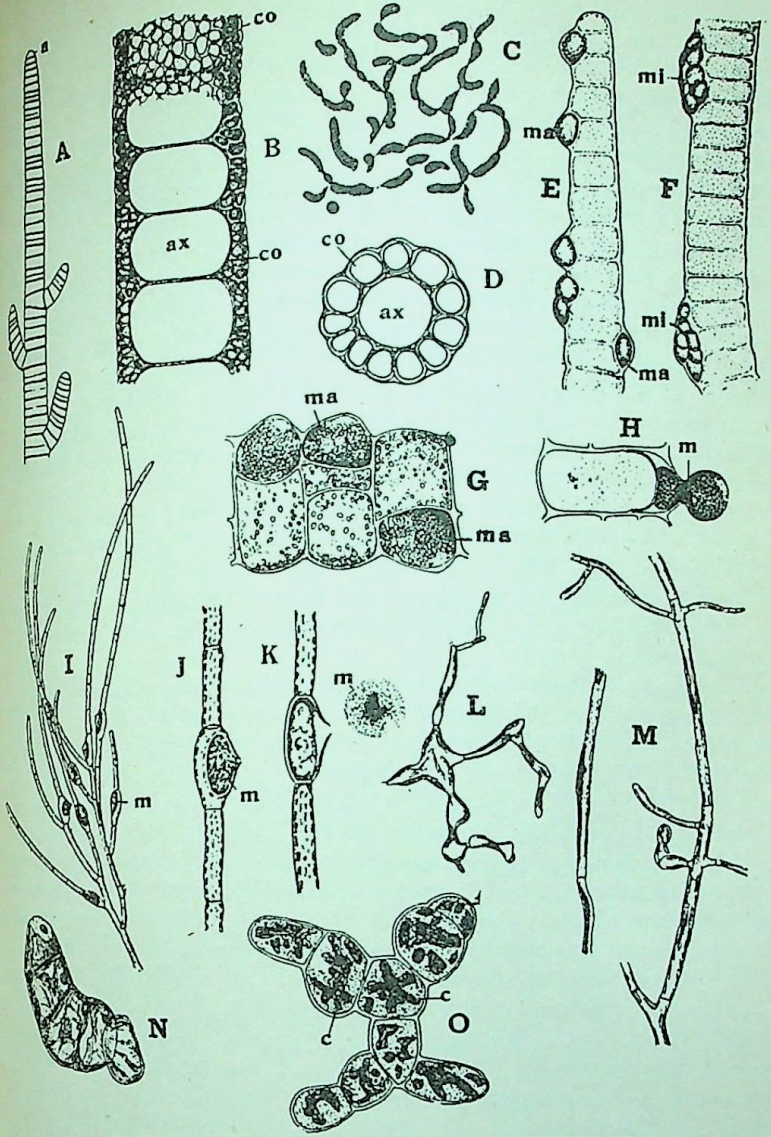

Fig. 146. A–H, *Compsopogon*; A, E–H, *C. caeruleus* Mont.; A, tip of a thread; E, F, threads with sporangia; G, small part of same, with macrosporangia (*ma*); H, liberation of spore; B, *C. aeruginosus* (J. Ag.) Kütz., part of older thread with cortex; C, the same, chromatophores; D, the same, older thread in section. I–K, *Rhodochaete pulchella* Thur.; I, thread with monosporangia; J, the same enlarged; K, liberation of monospore. L–O, *Conchocelis rosea* Batters; L, M, young growth; N, O, enlarged to show chromatophores. *a*, apical cell; *ax*, axial cells; *c*, chromatophores; *co*, cortex; *m*, monosporangia and monospores; *ma*, macrosporangia; *mi*, microsporangia. (A after Schmitz; B–D after Skuja; E–H after Thaxter; I–K after Bornet; L–O after Rosenvinge.)

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motionless, with dense contents and large nuclei. His so-called macrosporangia (fig. 146 E, *ma*) are always solitary, while the microsporangia (fig. 146 F, *mi*) for the most part form somewhat projecting sori(19). They develop either from the uncorticated cells or from those constituting the cortex. The macrosporangia, which are cut off by a curved wall (fig. 146 G, *ma*), liberate their contents through an aperture in the wall (fig. 146 H), after which the parent-cell enlarges and fills the cavity; this is very reminiscent of *Erythrotrichia*. Skuja ((114) p. 607), however, regards the macrosporangia as arrested branches and considers that they develop only under cultural conditions. According to his view the normal organs of multiplication are the microsporangia.

In the coloration of the chromatophores, the method of reproduction, and the absence of pit-connections between the cells there are indications of affinity with Bangiales and, in view of the varied development of the latter, it is not improbable that they might have evolved into more elaborate types. A renewed investigation of *Compsopogon* in tropical habitats may cast further light on this problematic form.

Reference should also be made to *Rhodochaete* ((14) p. 260, (110) p. 317), a minute marine epiphyte with simple branched filaments showing apical growth (fig. 146 I) and reproduction by monospores (*m*), produced in essentially the same manner as in *Erythrotrichia*. Small pits are stated to occur in the septa between adjacent cells. The affinities are very obscure.

Another uncertain member of Bangiales is *Conchocelis rosea* (4),[1] which lives in the shells of Molluscs or the tubes of Serpulids. It seems to be widespread in water of some slight depth in North Atlantic and Arctic seas ((63) p. 131, (95) pp. 54, 257, (103*a*) p. 111, (106) p. 618) where, together with Blue-green Algae of a similar habit, it is stated to play (90) a part in the erosion of limestone rocks. The young growth (fig. 146. L, M) consists of narrow threads composed of elongate cells of irregular shape; later the filaments branch richly and form a more or less continuous layer. According to Jónsson the cells contain a stellate chromatophore (cf. also (10) p. 349), but Rosenvinge ((106) p. 619) describes a number of ribbon-shaped ones (fig. 146 N, O, *c*); he also records small pit-connections between the cells. The fertile tracts are formed by short branched threads (fig. 146 N, O) which develop from swollen vegetative cells. The cells possess dense contents with plentiful starch and give rise to monospores.

Batters regarded this alga as closely related to *Erythrotrichia*, although *Colaconema* would perhaps be a better subject for comparison. The presence of pit-connections distinguishes it from the true Bangiales, but a reference to any particular group of Florideae is on present knowledge impossible.

[1] Nadson ((89) p. 36) regarded this alga as a form of *Ostreobium Queketii* Born. et Flah. (1, p. 426), but was probably confusing it with a red variety of the latter (cf. (95) p. 257).

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Sub-class II. Florideae

A. THE VEGETATIVE ORGANS

1. The general Features of Thallus-structure

The simple non-elaborated filament is rare among Florideae, being seen only in *Acrochaetium* (fig. 148 A–C) and its immediate allies (p. 450), as well as in certain Ceramiaceae.[1] The majority exhibit a more complex structure, although often remaining filiform in outward appearance, since elaboration is rarely associated with any great increase in bulk. Sections of such forms, however, often display a compact tissue which may show considerable differentiation. In Gigartinaceae and Delesseriaceae a foliose habit is developed, while certain families (Squamariaceae, Corallinaceae) consist largely or entirely of crust-forming types. The branching of the thalli, though often appearing dichotomous, is probably for the most part monopodial.

All Florideae, no matter how compact their structure, are composed of systems of richly branched threads ((192) p. 8, (586) p. 216). The latter may be but loosely connected and readily distinguishable (*Batrachospermum*, fig. 150 B, C; *Nemalion*, fig. 158 C, D) or they are so closely fitted together that the filamentous derivation is not easy to recognise (*Furcellaria*, fig. 163 A; *Chondrus*, fig. 175 A, B). The threads of most of the more loosely branched forms are embedded in

[1] For an epitome of the classification of Florideae, see p. 737.

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copious soft mucilage; in the more compact types this is denser and serves to connect the diverse units and their branches. In the filaments forming the basis of construction of the thallus it is often possible to distinguish (fig. 150 A) main axes of unlimited (*a*) and laterals of limited growth (*w*), the latter in many instances closely aggregated and commonly arising in opposite pairs or whorls from the cells of the main axes (cf. also fig. 154 C).

Two distinct, though closely related, variants of this type of structure are met with in primitive and more specialised groups alike, and there are few Florideae that cannot be referred to one type or the other. In the uniaxial forms (e.g. *Sirodotia*, fig. 150 A; *Gloeosiphonia*, fig. 153 B) the main axes (*a*) consist of a single row of often large cells; in the multiaxial types (e.g. *Nemalion*, fig. 158 D; *Platoma*, fig. 159 A) the axes (*a*, *m*) are composed of a number of parallel or subparallel threads. This is the only essential difference between the two (cf. (502) p. 254). The germinating spores of many Nemalionales and Cryptonemiales first give rise to a prostrate system (figs. 153 C, *bs*; 159 D, *b*), which is commonly discoid and produces more or less numerous erect threads (339, 379). It is by the further development of one (uniaxial) or of a group (multiaxial) of the latter that the erect thallus is produced. The structure of these forms is therefore based on a primary heterotrichous condition (1, p. 21), which is equally recognisable, though in a modified form, in the early stages of development of Gigartinales (figs. 167 I–K; 169 C) and Rhodymeniales (figs. 182 E, F; 183 D, E). Alone in Ceramiales, where the germlings appear invariably to lack a prostrate system (figs. 185 D–F; 194 D, E), is the heterotrichous habit altogether suppressed. In its dominance in the less specialised and its disappearance in the most advanced orders, the Florideae show a close parallel with Phaeophyceae (p. 21 and (770)).

Uni- and multiaxial construction are in general characteristic of distinct taxonomic units ((387) p. 104). All Rhodymeniales are multiaxial and all Ceramiales[1] uniaxial, but in other orders both types are represented in different families. Many Cryptonemiales are uniaxial, although the Corallinaceae, for instance, are multiaxial. In the Gigartinales the less specialised members (*Endocladia*, etc.) are uniaxial, while the more specialised Gigartinaceae are multiaxial. Kylin ((387) p. 46) regards the multiaxial state of these forms as secondary, but the basic heterotrichy affords the means for a ready passage from one type of construction to the other.

A second fundamental characteristic of the Florideae lies in the strict apical growth of the threads composing the thallus. This growth is effected by apical cells ((5) p. 11, (586) p. 217)[1] which are

[1] In a few Delesseriaceae (e.g. *Nitophyllum*, *Cryptopleura*) no central thread can be distinguished and growth is effected by division of the marginal cells (cf. p. 536).

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often dome-shaped (e.g. *Lemanea*, fig. 156 I, *m*) and cut off a single series of segments (*s*) parallel to the base, although in certain advanced types they are two- (fig. 166 A, C) or three-sided (fig. 167 A) and give rise to as many series of segments. The segments themselves usually cut off laterally two or more *pericentral cells* (fig. 154 F–H, *1–4*), which in many Florideae (not in most Rhodomelaceae) act as the apical cells of laterals; these are not uncommonly whorled (figs. 153 B, *l*; 154 D, E). The remainder of the segment, constituting the *central cell* (*a*), for the most part undergoes no further septation. Division walls passing through the axis of a segment, whether transverse or longitudinal, are formed only in a few special instances (Corallinaceae, some Delesseriaceae, (590) p. 112). In other words enlargement in Florideae is effected almost solely by apical growth, and there is usually no intercalary division of the segments (cf. also (380) p. 66, (519) p. 177, (599) p. 299).

As a result of this apical growth and of the formation of the thallus from juxtaposed filaments, the inner cells of most of the compact pseudo-parenchymatous types, which undergo no further division, become markedly stretched; they are often broad and considerably elongated, while towards the periphery the cells become progressively shorter and smaller (figs. 167 C; 175 B). The primary construction is often more or less obscured by the development, from various internal cells, of septate *hyphae* which push their way in all directions (often for the most part longitudinally, figs. 156 L; 166 F, *hy*) between the cells already present. In many compact forms the superficial layer, representing the apical cells of the ultimate branches of the filaments, is meristematic.

2. Pit-connections[1]

Genetically related cells, forming part of the same thread and derived from a common parent-cell by division, are in practically all Florideae connected by conspicuous pits in the septa; such *primary pits* are single and generally circular (figs. 139 B, *pi*; 147 H). They are stated to be lacking in *Batrachospermum* ((469) p. 231). The pits are distinguishable already in young septa and occupy the axis connecting the two daughter-nuclei. When first formed they are relatively narrow, and only attain their full width as the segment broadens. In some instances they occupy the entire septum (cf. fig. 147 M). Where not directly obvious, they can generally be rendered visible by treatment of the material with hydrochloric acid or caustic soda. The pit-membranes often stain with methyl green or saffranin. According to

[1] The abundant, mostly earlier, researches that failed properly to elucidate these structures cannot be considered here (cf. (192) p. 16; and (18), (305), (340) p. 296, (452), (466), (692) p. 100). Many older workers thought that the pits were open canals.

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Falkenberg ((192) p. 24) they react to stains in the same way as the "cuticle" at the surface of the alga.

The pit-cavities are occupied by broad cytoplasmic strands. Closely applied to either side of the pit-membrane one can often recognise two circular discs (cf. also (338) p. 100, (469) p. 232) staining readily with haematoxylin (fig. 147 J–M, *d*). Recent investigations (403,469) tend to show that the discs consist of a thickened peripheral ring containing pectic substances and supporting a delicate plasma-membrane; according to Celan (99) they contain lipoids. The discs are difficult to separate from the adjacent cytoplasm and are, according to many authorities,[1] connected by fine cytoplasmic strands (fig. 147 B, K, *pl*) which traverse the pit-membrane and are sometimes restricted to its periphery; others ((15) p. 177, (335) p. 23, (338), (469) p. 235) have denied the existence of such cytoplasmic connections. A sieve-like appearance of the pit-membrane has frequently been recorded ((192) p. 595, (291) p. 370, (742) p. 76). Schmitz regarded the discs as modifications of the cytoplasm lining the pit-membrane; they are separated from the vacuole by a layer of cytoplasm, which is often full of deeply staining matter and may show a fibrous structure ((192) p. 22, (524) p. 283). In plasmolysed cells the cytoplasm adheres to the discs which retain their position at the bottom of the pit-cavity. Jungers ((335) p. 23) concludes that the discs are part of the membrane; in *Griffithsia* and *Ceramium*, moreover, he claims that the pits consist of a single lenticular body (fig. 147 L) and that no separate pit-membrane is distinguishable.

The exact nature of the pit-connections thus remains undecided, and there is possibly some variety in structure. However that may be, they are probably of importance in the transport of food-material and perhaps also in conduction of stimuli.

Mangenot ((442); cf. also (99)), examining especially the gonimoblasts (p. 599) of diverse Ceramiales, denies the presence of a pit-membrane and describes certain differences between the discs on the two sides of the pit. Enlargement of the pit-connections is usual in the region of the developing cystocarps and this may be associated with disappearance of the intervening membrane (cf. (400) p. 32). The frequent presence of pit-membranes between the vegetative cells must, however, be regarded as established.

In diverse Ceramiales ((100), (151), (152), (466) p. 616, (524)) a strand of cytoplasm extends from pit to pit across the central vacuole (fig. 147 M, N), a feature which is specially obvious in the axial cells of certain species of *Ceramium*. When the threads fork, the strand assumes the form of a Y with three arms of about equal length; the older strands may become much attenuated. Tylose-like ingrowths from the cortical into the axial cells have been recorded in *Ceramium rubrum* ((524) p. 289).

[1] See (141) pp. 142, 164, (192) p. 11, (232) p. 105, (352) p. 344, (428) p. 642, (457), (586) p. 218, (599) p. 300.

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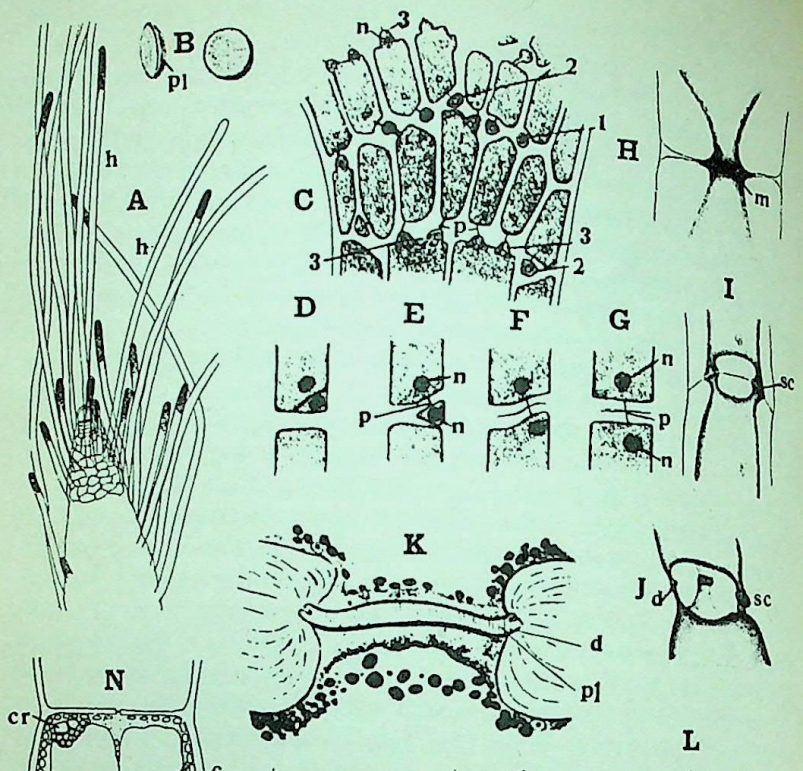

Fig. 147. A, *Gloeosiphonia capillaris* Carm., apex with unicellular hairs (*h*). B, H–J, *Rhodomela subfusca* (Woodw.) C. Ag., pit-connections, in B from the surface. C–G, *Polysiphonia violacea* (Roth) Grev.; C, part of thread in surface-view showing various stages (*1–3*) of formation of secondary pit-connections; D–G, successive stages in formation of a secondary pit-connection. K, *Bornetia secundiflora* (J. Ag.) Thur., pit-connection in section. L, *Griffithsia setacea* (Ellis) Ag., ditto. M, *Ceramium echionotum* J. Ag., axial cell with median cytoplasmic strand. N, *Heterosiphonia plumosa* (Ellis) Batt., single cell showing the same. *as*, axile cytoplasmic strand; *c*, chromatophore; *co*, cortical cell; *cr*, crystalloid; *d*, discs of pit-connection; *h*, hair; *m*, pit-membrane; *n*, nucleus; *p*, pit-connection; *pl*, plasmodesmae; *s*, starch; *sc*, secondary pit-connections; *sp*, spine. (A after Rosenvinge; K after Miranda; L after Jungers; M, N after Phillips; the rest after Falkenberg.)

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In the more compact types, where the close juxtaposition of the threads obscures the filamentous construction, the pit-connections are often of great value in tracing the genetic relationship of adjacent cells.[1] Many of the more specialised forms, however, sooner or later develop *secondary pit-connections* ((586) p. 218) between unrelated cells, no doubt in response to special physiological requirements, especially longitudinal transmission of food-material. Such secondary connections are unknown in Nemalionales and Ceramiaceae, as well as in diverse of the less specialised Cryptonemiales and Gigartinales ((400) p. 29).[2] Their mode of development is readily studied in overlying pericentral cells of *Polysiphonia*, especially in those species that develop thick membranes at an early stage ((192) p. 13, (549), (551)).

In the first place the nucleus passes to the lower end of the cell and then divides, whereupon one of the daughter-nuclei, together with a small amount of cytoplasm, is cut off by an oblique wall (fig. 147 D). The newly formed septum progressively thickens (fig. 147 E) so that the small daughter-cell is gradually pushed towards one of the underlying pericentrals (fig. 147 C, *1*, *2*); meanwhile a pit-connection (*p*) becomes obvious between the pericentral and the daughter-cell. Ultimately the latter comes into contact and fuses with the pericentral below (fig. 147 C, *3*), the pit-connection (*p*) now linking the two superposed pericentrals (fig. 147 F), each of which thus contains two nuclei, one at the upper and the other at the lower end. The septum soon assumes a horizontal position (fig. 147 G). In some Ceramiales (e.g. *Rhodomela subfusca*, fig. 147 I, J) several secondary pit-connections may be formed between adjacent cells (cf. also (380) p. 70).

3. Hairs

The peripheral cells in the younger parts of the thalli of many Florideae bear a more or less dense growth of elongate unicellular colourless hairs (fig. 147 A) that sometimes reach a length of a millimetre or more ((37) p. 675, (465) p. 75, (559) p. 207). In certain families (Gigartinaceae, Phyllophoraceae, Delesseriaceae) they are altogether wanting, while in Rhodomelaceae their place is taken by the trichoblasts (p. 544); in some Florideae (*Rhodymenia palmata*) they are confined to definite areas ((558) p. 572, (745) p. 103). Although usually deciduous, they sometimes persist even on the older parts (e.g. *Callithamnion corymbosum*). The hairs are mostly thin-walled, with a delicate layer of cytoplasm surrounding the central vacuole; chro-

[1] Schmitz ((590) p. 111) recommends boiling in water or dilute glycerine and then staining with nigrosine. Kylin ((380) p. 5) advocates soaking of compact types for 1–24 hours in 1 % hydrochloric acid, followed by clearing in dilute caustic soda for some hours. The thallus can then be squeezed out on a slide.

[2] They are also lacking in most Corallinaceae and, where they occur, are formed in a different manner (cf. p. 509).

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matophores are generally lacking, although small faintly coloured ones are sometimes (*Plumaria elegans*, *Spermothamnion*) found in the young hairs.[1]

In northern waters such hairs are most abundant in spring and early summer and are often completely lacking in winter. The extent of their development is usually (cf. however, (559) p. 213) unrelated to the depth at which the alga grows, although in the Mediterranean ((37) p. 679) they are stated to be best developed in well-illuminated situations. According to Berthold they constitute a protection against intense illumination, and it cannot be denied that they may fulfil such a rôle, although it is doubtful whether that is their most important function. Diverse authorities ((379) p. 11, (503) p. 391, (559) p. 214), in view of their frequent restriction to the growing parts and the large surface they present, have emphasised their probable importance in absorption of nutriment. Such a function is also in accordance with their prevalence in the early part of the growing season and in well-illuminated situations. Kylin ((379) p. 11) in *Dumontia incrassata* found that hair-development only took place in cultures to which nitrates had been added.

4. Simple Filamentous Types

The most primitive structure among Florideae is found in *Acrochaetium* (*Chantransia*)[2] and *Rhodochorton*,[3] both members of the Nemalionales with a wide distribution in the sea, although of the former one or two freshwater species are known; these are sometimes referred to a separate genus *Audouinella* (cf. (262) p. 45, (649) p. 127, (727) p. 191), but there appear to be no adequate grounds for separation ((643) p. 177). Certain species of *Acrochaetium*[4] possess a heterotrichous habit (e.g. *A. Daviesii*, fig. 148 A; (276) pl. 314; *A. attenuatum*, fig. 148 B; *A. Hauckii* Schiffner (577) p. 133), while others are erect and attached by a well-marked basal cell (e.g. *A. parvulum* (Kyl.)

[1] Regarding the hairs of *Gracilaria* and Corallinaceae, see pp. 488, 507.

[2] Incl. *Balbiania* ((262) p. 49, (632)). De Candolle's genus *Chantransia* comprised a diversity of forms (Green Algae, stages in the development of diverse Nemalionales (*Batrachospermum*, *Lemanea*, see pp. 455, 466), etc.), but did not include any of the marine forms now referred to *Acrochaetium*. This genus was established by Naegeli ((478) p. 402) for species until then referred to *Callithamnion*, which Thuret ((411) p. 106) included in *Chantransia* (cf. also (587)). Bornet's suggestion (66) that the name *Acrochaetium* should be reserved for species possessing sporangia only has rightly not met with favour. There can be little doubt that the name *Chantransia* should be abandoned (cf. also (8) p. 45, (34) p. 58, (50) p. 12, (262) p. 44).

[3] *Rhodochorton* has been regarded as a member of Ceramiales, but the evidence is in favour of a close affinity with *Acrochaetium*. Drew ((175) p. 148; cf. also (565) p. 5) even places all the species of the latter in the genus *Rhodochorton*.

[4] See (175), (263) p. 99, (368), (369), (387), (424) p. 33, (425) p. 83, (470), (558), (701) p. 65.

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Hoyt; cf. fig. 148 C). Most are epi- or endophytes on other marine Algae, but a number occur on Hydroids ((113), (323) p. 116), Bryozoa

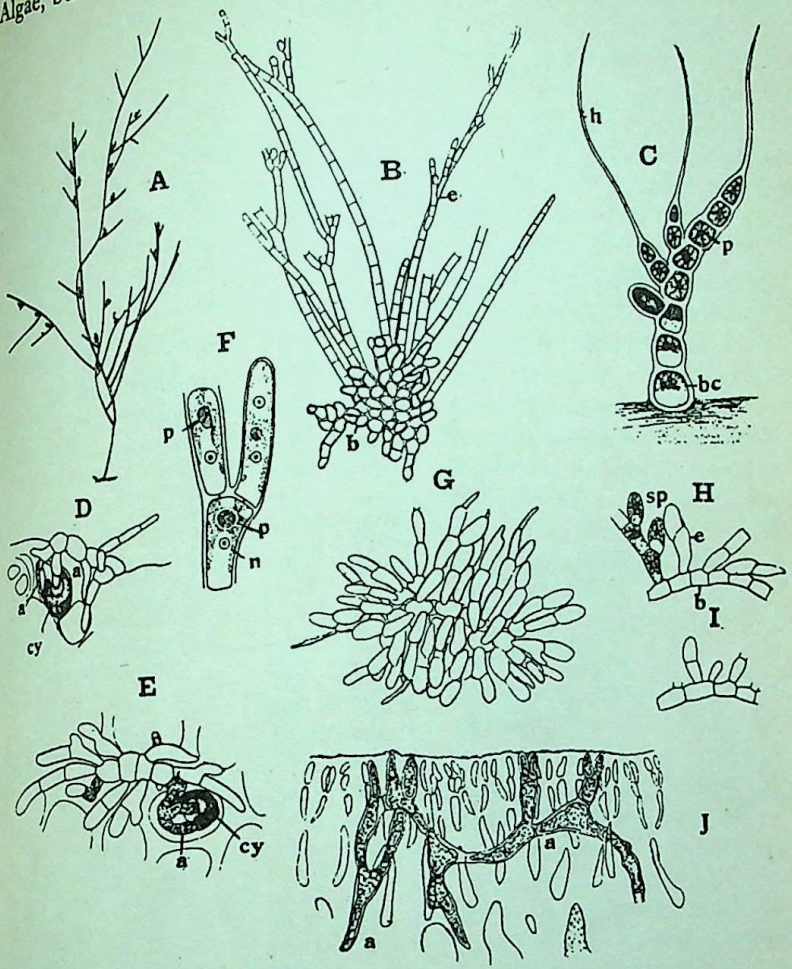

Fig. 148. *Acrochaetium*. A, *A. Daviesii* (Dillw.) Naeg., entire plant with monosporangia. B, *A. attenuatum* (Rosenv.), showing the heterotrichous habit. C, *A. crassipes* Boerges. var. *longiseta* Boerges., showing axile chromatophores. D, E, *A. cytophagum* (Rosenv.), reduced forms, with threads (*a*) within the cytoplasm (*cy*) of the cells of *Porphyra*. F, *A. rhipidandrum* (Rosenv.), cell-structure. G–I, *A. humile* (Rosenv.); G, from the surface; H and I, in profile. J, *A. Polyides* (Rosenv.) showing endophytic threads (*a*). *b*, basal (prostrate) system; *bc*, basal cell; *e*, erect system; *h*, hair; *n*, nucleus; *p*, pyrenoid; *sp*, sporangium. (A after Taylor; C after Boergesen; F after Kylin; the remainder after Rosenvinge.)

(160), Sponges ((727) p. 195), or on the shells of Molluscs; *A. efflorescens* is often found on stones. Some are exceedingly minute (e.g. *A. trifilum* (Buffh.) Batt.; *A. minimum* Collins (139)).

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The mode of germination of the spores shows great diversity.[1] In certain species they produce a prostrate system (sometimes a pseudo-parenchymatous disc) bearing the erect threads; no traces of the original spore are recognisable in the mature plant (fig. 148 B). Commonly, however, the spore persists (fig. 148 C) as a prominent basal cell (*bc*), which either constitutes the only means of attachment to the substratum (fig. 148 C; (51) p. 13, (368) p. 124) or also produces radiating prostrate filaments (*A. efflorescens*, *A. violaceum*, (177) p. 441, (558) p. 81), from which further erect threads may arise; in some of the endophytic forms these secondary filaments penetrate into the substratum ((51) p. 28). In *Kylinia* ((424) p. 41, (438) p. 245, (558) p. 141), a minute epiphyte, the entire plant consists of a system of procumbent threads arising on all sides from the attaching cell and bearing terminal sporangia. The heterotrichous types are no doubt the most primitive. All species of *Rhodochorton* (fig. 149 A) are heterotrichous, the basal system (*b*) being commonly discoid.[2]

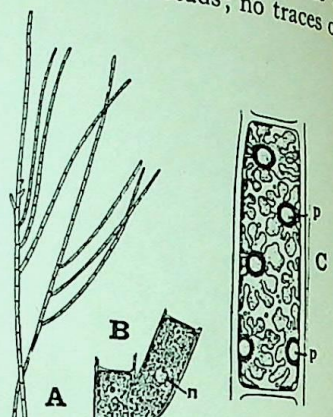

Fig. 149. *Rhodochorton*. A, B, *R. Rothii* (Turt.) Naeg. (after Taylor); A, habit; B, cell-structure. C–E, *R. floridulum* (Dillw.) Naeg., cell-structure (after Kuckuck). *b*, prostrate and *e*, erect systems; *n*, nucleus; *p*, pyrenoid.

Both in *Acrochaetium* and *Rhodochorton* the branches arise near the top of the parent-cell (fig. 149 B). In *Acrochaetium* they commonly terminate in hyaline hairs (fig. 148 C, *h*) which mostly fall off at an early stage. If branching continues, a sympodial construction may arise ((368), (369) p. 115, (559) p. 211), the lateral displacing the hair and the part of the axis below it. In certain species (*A. efflorescens*) the cells of the erect threads produce septate rhizoids which aid in attachment to the substratum.

The cells of *Acrochaetium* usually possess a single axile (fig. 148 C) or parietal (fig. 148 F) chromatophore containing a pyrenoid (*p*; (368)

[1] See (51) p. 21, (66) p. xviii, (113), (129) p. 302, (263) p. 100, (264) p. 173, (558) p. 81.

[2] See (45) p. 389, (129) p. 308, (202) p. 268, (359) p. 345, (540) p. 59, (553) p. 791, (554) p. 23, (555), (558) p. 388, (701) p. 63.

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p. 122, (558) p. 82). The parietal chromatophores show considerable diversity, often appearing as plates (fig. 148 F) or cylinders which are frequently lobed (*A. corymbiferum* ((389) p. 5) and may be protruded into the cell-cavity. In some species (*A. efflorescens*) there are commonly several chromatophores[1] which may be spirally twisted and provided with a number of pyrenoids (cf. also (154), (410) p. 4). In *Rhodochorton* ((31) p. 389, (359) p. 344, (478) p. 355) the cells mostly contain several chromatophores which are either stellate with a central pyrenoid (*R. floridulum*, fig. 149 C, D; (276) pl. 120 A) or band-shaped and without pyrenoids (*R. Rothii*, fig. 149 B; *R. membranaceum* Magnus). The lobes of the stellate chromatophores expand at their tips and may fit together to form an almost continuous parietal layer (fig. 149 E). In *R. islandicum* Rosenv. the cells contain numerous small chromatophores.

In the endophytic species of *Acrochaetium* the erect system commonly consists merely of short threads bearing the sporangia or it may be altogether suppressed ((160), (358) p. 391, (460) p. 277, (558) p. 82). Similar reduced types are found among the epiphytes ((50) p. 24; fig. 148 G–I) and constitute an interesting parallel with *Ectocarpus* (p. 55). The endophytic filaments are often of considerable length (fig. 148 J, *a*) and are probably for the most part intercellular, but *A. cytophagum* ((558) p. 121; fig. 148 D, E) seems to be definitely parasitic, short laterals (*a*) penetrating into the cells (*cy*) of the host (cf. also (175) p. 153). In *A. endozoica* (Darb.) Hamel, where the elongate endophytic threads give rise at intervals to erect tufts, some of their branches are stated to penetrate into the living polyps. It has been suggested ((558) p. 82) that *Colaconema* (p. 424) may belong here.

The erect threads of *Rhodochorton* usually branch, especially towards the tips (fig. 149 A). Several species occur on sand- and mud-covered rocks between tide-levels. The minute tufts of *R. Rothii* ((276) pl. 120 B, (279)) are specially characteristic of the intertidal region and are often found at and above high-water mark, as well as in caves and other feebly lighted situations; at lower levels the tufts are longer. The basal system of *R. membranaceum* (fig. 235 H; *Callithamnion membranaceum* Magnus (440) p. 67, (558) p. 393) inhabits the chitinous walls of diverse hydroids. In *R. islandicum* Rosenv. (555), which forms a violet-red felt in caves, the lower cells grow out into almost colourless stolons producing further erect tufts and possibly serving for vegetative propagation. The heterotrichous habit speaks against a reference of this genus to Ceramiales.

Callithamnion and certain of its allies, though showing a filamentous structure, similar to that of the genera of Nemalionales just considered, have, like other Ceramiales, lost all traces of heterotrichy. The simple structure is probably the result of specialisation (see p. 523).

[1] For such species, which are also distinguished by seriate carpospores, Rosenvinge ((558) p. 88) creates the subgenus *Grania*.

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5. The simpler Types of Uniaxial Construction and their Elaboration

The classical example of a simple uniaxial red alga is afforded by the freshwater *Batrachospermum* (sometimes called the "frog-spawn" alga), from which *Sirodotia* (p. 610) does not differ appreciably in

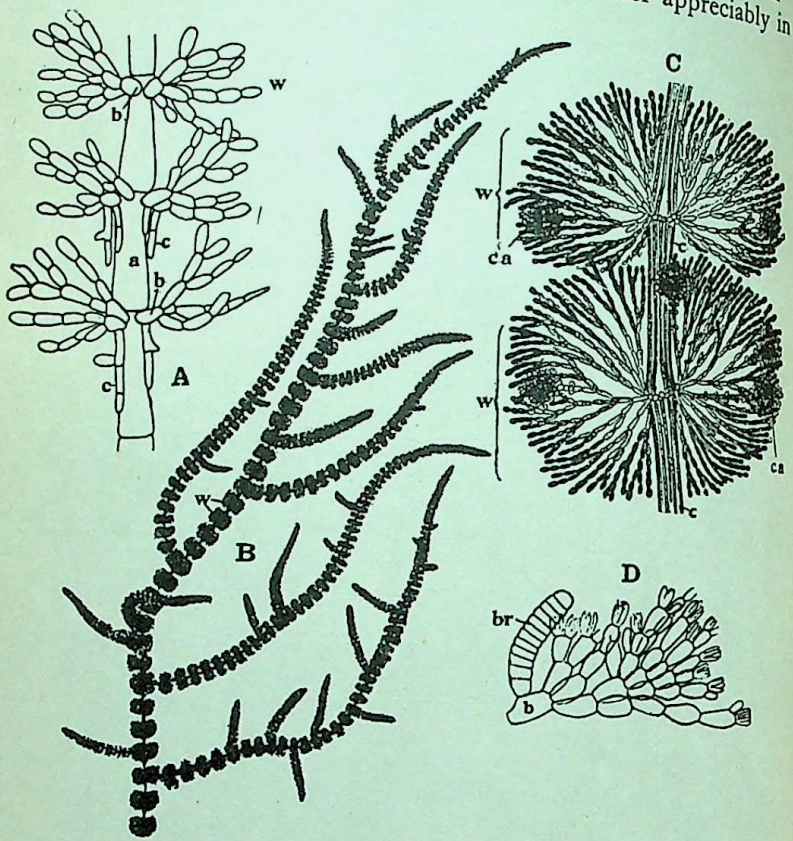

Fig. 150. A, *Sirodotia suecica* Kylin, three whorls with cortical threads. B, C, *Batrachospermum moniliforme* Roth; B, habit; C, two whorls enlarged. D, *B. vagum* (Roth) Ag., origin of long branch (*br*) from basal cell of lateral. *a*, axial cell; *b*, basal cells of laterals; *c*, cortical threads; *ca*, carposporangia; *w*, whorls of laterals. (A after Kylin; the rest after Sirodot.)

vegetative characters. To the naked eye the mucilaginous growths of many *Batrachospermums*[1] appear as chains of delicate beads (e.g. *B. moniliforme*, fig. 150 B). The thalli, which are violet or blue-green in colour, show monopodial (often pseudo-dichotomous) branching and may be 20 or more centimetres in length. When magnified (fig. 150 C), each "bead" is seen to consist of a whorl (*w*) of densely

[1] See (71), (132) p. 471, (223), (262) p. 281, (370), (510) p. 169, (512), (631), (633).

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branched laterals of limited growth, all of about the same length. The laterals arise just below the septa (fig. 150 A) separating the elongate cells of the main axes (*a*). The cells contain a number of parietal chromatophores with pyrenoids.

The apical cells of the long axes (fig. 151 A, *a*) cut off a single series of segments (*s*) which rapidly widen and lengthen, usually remaining broadest at the septa (fig. 150 A, C). The laterals consist of small, ellipsoidal or moniliform cells, and the ultimate branches commonly terminate in hairs, surrounded by a basal sheath formed from the split outer layer of the membrane of the bearing cell ((378) p. 163, (465) p. 76, (582) p. 134); in certain species (e.g. *B. Dillenii* Bory, *Sirodotia*) the laterals remain very short. The members (frequently 4–6) of a whorl are formed successively from the pericentral cells (p. 446) cut off from the parent-segment, while further branches of unlimited growth (fig. 150 D, *br*) arise singly from the basal cell (*b*) of one member of a whorl. These cells also give rise to cortical threads (fig. 150 A, *c*), which grow downwards over the cells of the main axes and completely hide them from view (fig. 150 C, *c*); in some species of *Batrachospermum* and *Sirodotia* ((640) p. 299) they form a several-layered envelope. Towards the base of the plant these threads extend to the substratum, where they aid in attachment and augment the prostrate system (631). The threads enveloping the axial cells commonly give rise to secondary whorls, which may be so numerous that the beaded appearance is almost entirely lost (e.g. *B. vagum* (Roth) Ag.).

Species of *Batrachospermum* are widely distributed and usually favour the well-aerated water of slow-moving streams ((82) p. 45) or the margins of lakes, where there is not much change of temperature. Some favour the pools of peat-moors (*B. vagum* (370) p. 11), but usually occur where there is a spring ((732) p. 424). In most the mature shoots are annual, but in a few (*B. vagum*, *B. densum* Sirod.) they are perennial. Iltis (325) describes an interesting association between *B. vagum* and the snail *Planorbis planorbis* L.

Germinating carpospores are not uncommonly found entangled among the threads of the parent. The mode of germination ((129) p. 314, (240), (506) p. 113, (582) p. 132, (631) p. 143) is one which is frequent among Nemalionales. A process arises on one side (seemingly always the morphological base (240) p. 4, (582) p. 132), during which the delicate outer membrane of the spore is ruptured. Most of the cytoplasm passes into the process which is cut off by a septum (fig. 151 C, D) and undergoes transverse division (fig. 151 E) to form a creeping filament. The latter soon branches and gives rise to a prostrate system (fig. 151 B, *b*) bearing erect branched threads (*e*) which strongly resemble those of an *Acrochaetium*; this is the so-called *Chantransia*-stage ((71), (370) p. 10, (512), (631) p. 134, (633) p. 100). In feebly illuminated habitats ((631) p. 135) further development may be arrested for long periods and, since abundant propagation of this

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juvenile stage is effected by monosporangia (fig. 151 B, *m*) resembling those of *Acrochaetium* (p. 623), such stages were in the past regarded as independent species and referred to the genus *Chantransia* (p. 450).[1] Monospores may be formed in quite early stages (fig. 151 G). The *Chantransia*-stages are stated ((643) p. 174) to show certain differences from *Acrochaetium* in colour and mode of branching. Those of *Sirodotia* altogether resemble those of *Batrachospermum* ((640) p. 302).

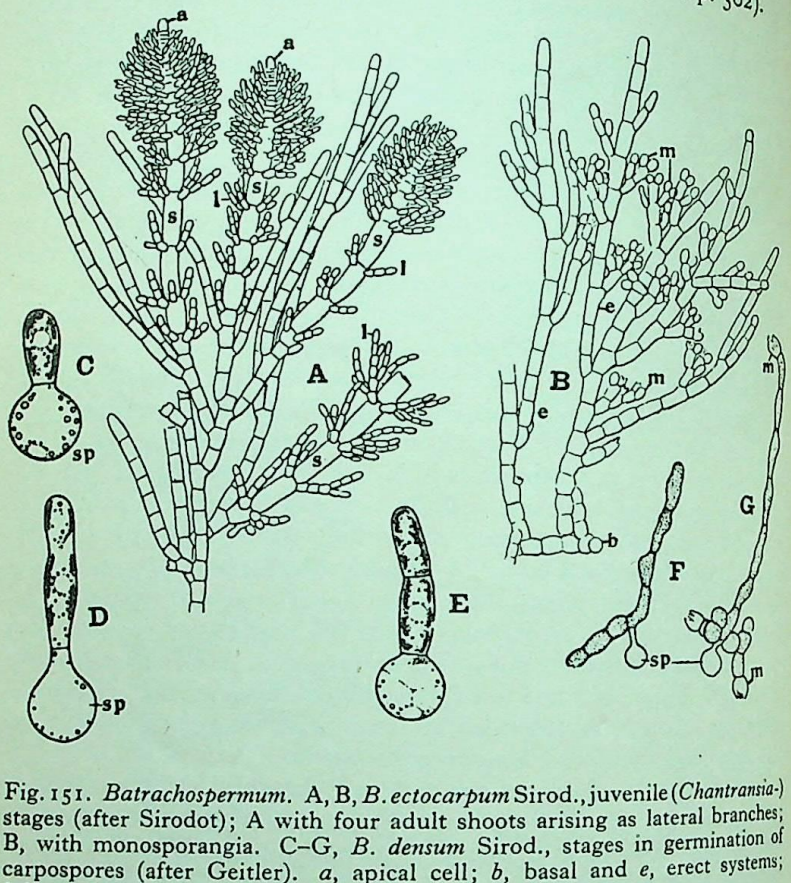

Fig. 151. *Batrachospermum*. A, B, *B. ectocarpum* Sirod., juvenile (*Chantransia*-) stages (after Sirodot); A with four adult shoots arising as lateral branches; B, with monosporangia. C–G, *B. densum* Sirod., stages in germination of carpospores (after Geitler). *a*, apical cell; *b*, basal and *e*, erect systems; *l*, lateral branches; *m*, monosporangia; *s*, segment; *sp*, monospore.

As a general rule adult shoots, recognisable by their broad squat cells, arise from the chantransioid stages before they have developed very far. They usually originate from one of the erect filaments or from a branch of such a filament (fig. 151 A); they may, however, arise directly from the prostrate system ((71) p. 283, (73) p. 306, (355)). Largely, it is to be supposed, because of the frequent persistence of

[1] Here belong *C. chalybea*, *C. pygmaea*, etc. (cf. (73)). Since such forms are often found apart from the mature plant, Brand ((74) p. 112) proposed the name *Pseudochantransia* for them.

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Chantransia-stages, they have been compared to the protonema of Mosses. This is justifiable, but it must be realised that they differ in no fundamental respect from the juvenile stages of diverse other less specialised Florideae ((770) p. 405) which are likewise heterotrichous and which commonly produce erect branches (fig. 153 C), apart from those giving rise to the mature plant (*m*); they may also bear sporangia.

The erect threads of the "*Chantransia*-stages" not uncommonly produce descending rhizoids which spread over the substratum and, together with the cortical threads of the adult shoots, serve to extend the prostrate system. These rhizoids may bear erect branches closely resembling the secondary laterals formed from the cortical threads of the mature plant ((71) p. 282). In *B. Breutelii* ((642) p. 359), from the Cape, the robust thick-walled erect threads of the chantransioid stage exhibit whorled branching and are covered below with a dense envelope of cortical threads from which secondary laterals may be formed.

The type of mature structure seen in *Batrachospermum* is repeated with some modifications in diverse marine Florideae (cf. fig. 152 C), all with cylindrical branched thalli. In most of these, however, as a result of the denser juxtaposition of the whorls, a beaded appearance is not manifest, and the branches of the laterals of limited growth form a continuous, though not usually very closely compacted, envelope (cortex) to the long axes. Examples are afforded by *Atractophora hypnoides* ((68) p. 50, (147), (387) p. 12, (478) p. 388, (766) p. 397; fig. 152 G) among Nemalionales; the Mediterranean *Thuretella* ((69) p. 185;[1] fig. 152 C–E), *Gloeosiphonia* (see p. 459), *Acrosymphytum purpuriferum* (J. Ag.) Kyl.[2] ((39) p. 12), and *Dudresnaya* among Cryptonemiales; *Calosiphonia* ((39) p. 3, (68) p. 38, (389) p. 37) among Gigartinales; as well as *Crouania attenuata* (Bornem.) Ag. ((50) p. 230, (272) p. 226, (276) pl. 106, (478) p. 384) and *Wrangelia penicillata* ((69) p. 183, (386), (478) p. 382, (766) p. 373; fig. 152 A, F) among Ceramiales. Most of these are commoner in the warmer seas.

The vegetative differences are not considerable. Most have a dome-shaped apical cell, but in *Wrangelia* (fig. 152 B) the segments (*s*) are oblique and cut off in succession five pericentrals, the first being always formed on the higher side of the segment which is situated alternately to right and left (*l*). The first pericentral gives rise to the most vigorous lateral of the whorl (fig. 152 A, *ml*), and it is from its basal cell (*b*) alone that the distichous branches of unlimited growth (*la*) are produced. Essentially the same structure is seen in *Schimmelmannia* ((389) p. 14, (599) p. 506, (634) p. 15), a member of Cryptonemiales with flattened pinnately branched thalli found in warmer seas. In *Thuretella*, *Dudresnaya*, *Atractophora* (fig. 152 G, *la*), *Calosiphonia* and *Schimmelmannia* the branches of unlimited growth arise direct from one member

[1] As *Crouania Schousboei* Thur.

[2] *Dudresnaya purpurifera* J. Ag. The genus *Acrosymphytum* was established by Sjöstedt ((634) p. 8; cf. also (499) p. 106).

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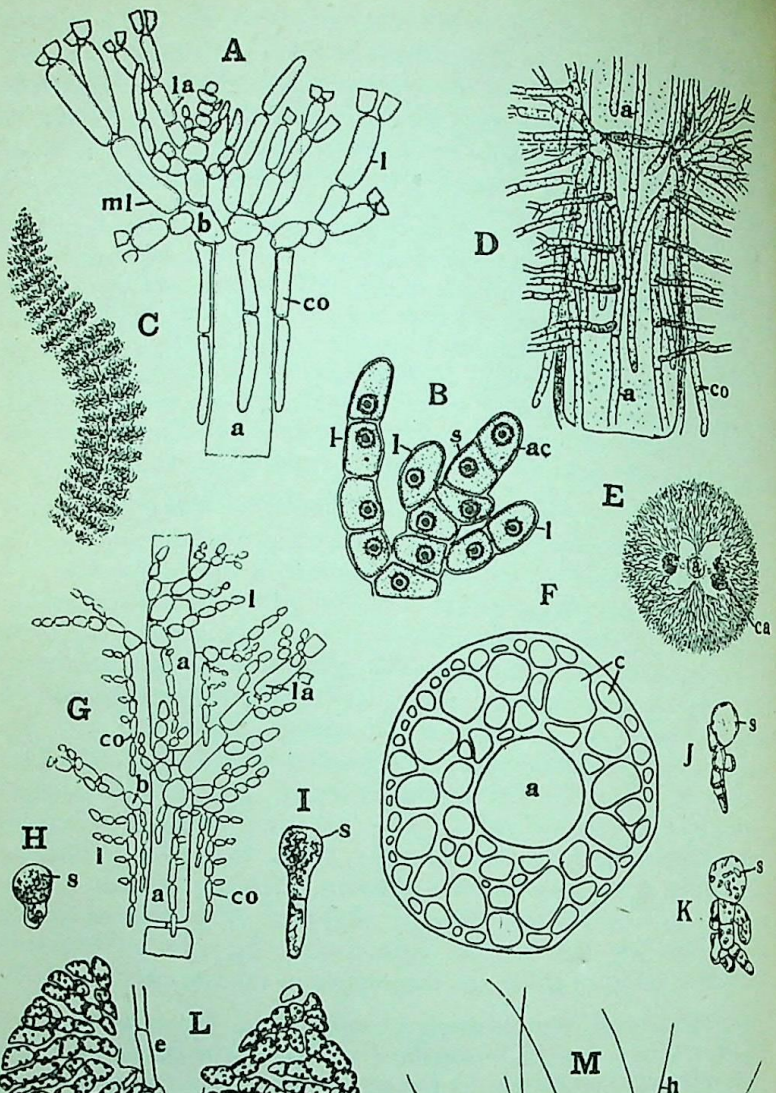

Fig. 152. A, B, F, *Wrangelia penicillata* C. Ag.; A, part of a whorl with underlying axial cell (*a*); B, apical cell (*ac*) showing mode of segmentation and formation of laterals; F, transverse section through a mature part of the thallus. C–E, *Thuretella Schousboei* (Thur.) Schmitz; C, small part of thallus; D, parts of two axial cells (*a*) showing the bases of a whorl of laterals

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of the whorl, in the last from the first lateral of each whorl; in *Calosiphonia* the laterals arise from the middle of the axial cells. The thick-walled axial cells of *Crouania* bear only three members in each whorl. In *Dudresnaya coccinea* ((39) p. 3) the lower cells of the primary laterals subsequently enlarge almost to the size of the axial cells, while the abundant cortical threads likewise become large-celled; as a result the mature structure simulates a multiaxial one. In the older parts of *Wrangelia* the laterals are shed and their basal cells become covered by a thick envelope of cortical threads (fig. 152 A, *co*; F, *c*). In *Atractophora* (fig. 152 G) and *Thuretella* (fig. 152 D) the latter bear numerous branches (*l*) so that a relatively compact cortex is formed.

In the early development of *Dudresnaya* ((106) p. 167, (129) p. 356, (339) p. 237, (695) p. 10) the protuberance from the spore (fig. 152 H, I) gives rise (J, K) to a prostrate system of richly branching threads which soon unite to form a compact disc (L) growing mainly at its forward margin. Most of the numerous erect threads (M) terminate in hairs (*h*), but some continue growth and produce the mature thalli (*m*); according to Killian ((339) p. 240) the latter are lateral branches of erect threads (cf. *Batrachospermum*). The early stages of *Atractophora* ((108) p. 274, (129) p. 321) are similar, although here the germinating spore divides by a vertical wall and remains recognisable within the prostrate disc that develops by outgrowth of the two cells; creeping threads arising from the peripheral cells divide at their tips to form secondary discs.

As an example of firmer construction among these uniaxial types *Gloeosiphonia capillaris* ((68) p. 41, (276) pl. 57, (389) p. 10, (478) p. 387, (634) p. 13) may be described in somewhat greater detail; the richly branched thalli usually grow submerged. The apical cell (fig. 153 C, *m*) divides like that of *Batrachospermum*, but the laterals arise from the middle of the axial cells. Each of these (fig. 153 B, *a*) produces a whorl of four laterals (*l*), the large basal cell (*b*) of which bears a number of one-celled branches spreading out in the horizontal and vertical planes. These secondary branches in their turn give rise to others with progressively smaller cells, the ultimate ramifications uniting, both in the transverse and longitudinal directions, with those of other adjacent laterals to form a cortex (*co*) covered by a well-defined surface-layer (*s*), the cells of which contain numerous branched ribbon-shaped chromatophores ((558) p. 277). The points of contact between the branch-systems of successive whorls are commonly visible as darker transverse bands on the surface of the thallus. The younger parts bear numerous hairs (fig. 147 A).

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and cortical threads (*co*); E, transverse section through a whorl, with two fruits. G, *Atractophora hypnoides* Crouan, small part of thallus. H–M, *Dudresnaya* sp., germination of spores and juvenile stages; H–K, successive stages in germination; L, basal system; M, juvenile stage, with two adult shoots (*m*). *a*, axial cells; *b*, basal cells of laterals; *c*, cortex; *ca*, carposporangia; *co*, cortical threads; *e*, erect thread; *h*, hairs; *l*, laterals of limited and *la*, of unlimited growth; *ml* (in A), first lateral of whorl; *s*, carpospore. (C–E after Bornet & Thuret; H–M after Killian; the rest after Kylin.)

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The cortical threads, which arise both from the basal cells of the laterals and from the central cells, are almost colourless and therefore

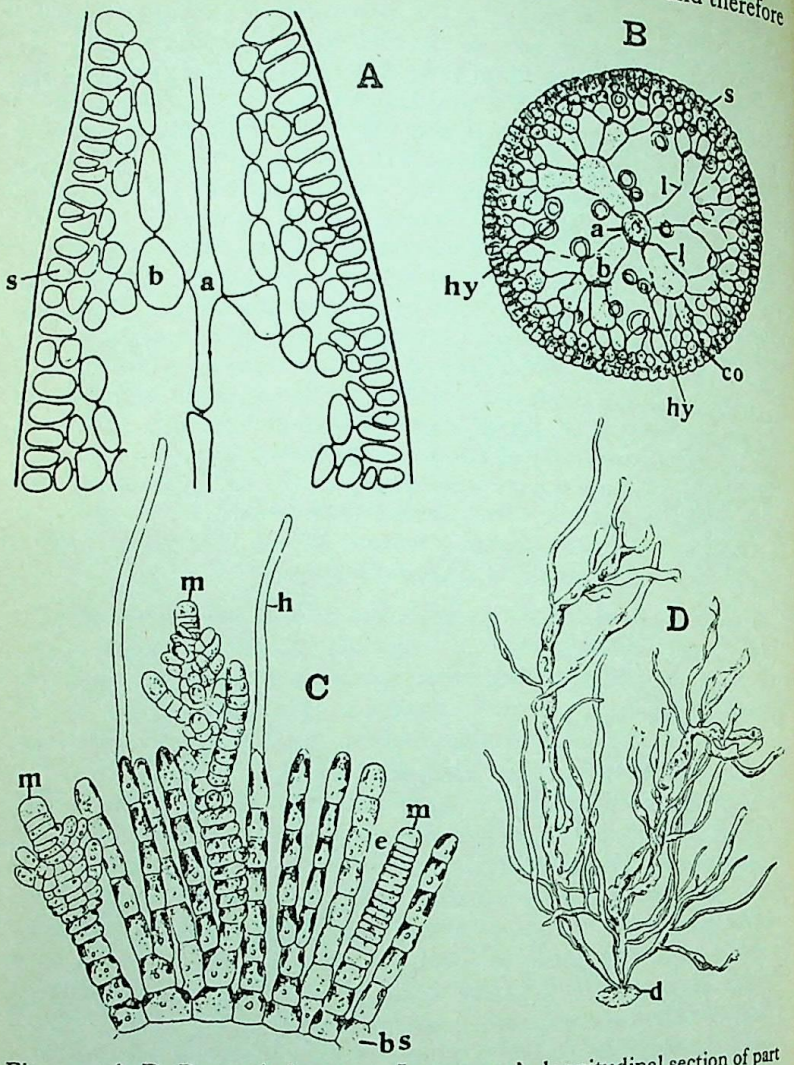

Fig. 153. A, D, *Dumontia incrassata* Lamour.; A, longitudinal section of part of thallus; D, habit. B, C, *Gloeosiphonia capillaris* Carm.; B, transverse section of thallus; C, juvenile stage showing development of three adult shoots (*m*). *a*, axial cells; *b*, basal cells of laterals; *bs*, basal system; *co*, cortex; *d*, basal disc; *h*, hairs; *hy*, hyphae; *l*, laterals; *s*, surface-layer of thallus. (A after Kylin; B after Bornet & Thuret; C after Kuckuck from Oltmanns; D after Taylor.)

more appropriately spoken of as hyphae. The majority occupy the interspaces between the laterals (fig. 153 B, *hy*) and later form a dense weft on the inner surface of the cortex, thus increasing the rigidity of

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the peripheral cylinder. This is the more necessary, as the axial cells and the basal cells of the laterals disintegrate in older parts. Some of the hyphae produce secondary laterals which push between the primary whorls and add to the density of the cortex.

The early stages of germination ((77) p. 288, (129) p. 353, (558) p. 277) resemble those of *Batrachospermum*, although the original spore is stated to retain its contents. The primary filament gives rise to a one-layered disc which no doubt corresponds to the basal crust described by Kuckuck ((363) p. 199, (502) p. 242). This (fig. 153 C, *bs*) bears numerous short erect threads (*e*), often crowned by a unicellular hair (*h*), and the mature thalli (*m*) are formed from one or more of these threads or their branches (cf. *Dudresnaya*, p. 459). *Gloeosiphonia* probably hibernates by means of these crusts ((558) p. 278).

The common seaweed *Dumontia incrassata* (*D. filiformis* Grev. ((183), (276) pl. 59, 357 B, (380) p. 10, (475) p. 243, (558) p. 155), which likewise belongs to Cryptonemiales, shows an even firmer construction of essentially the same type (fig. 153 A); the hyphae often form secondary pit-connections (p. 449) with other cells of the thallus. The branched fistular thalli (fig. 153 D), which may be a centimetre or more thick, arise from a broad perennial (cf. however (741)) basal crust (*d*). This (cf. also (76), (363) p. 199, (379) p. 9, (538) p. 26) consists of close-set vertical threads showing little branching and arising from a one-layered prostrate system. Certain parts of the crust may grow more actively and come to overlie others so that several strata may be recognisable (cf. *Ralfsia* among Phaeophyceae); by similar local growth the base of the annual frond becomes embedded in the crust after the upper part has disintegrated. The adult thallus is formed from one of the erect threads.[1] The germinating spores ((129) p. 368) divide to form a compact cushion of cells bearing long unicellular hairs.

The slight compression evident in *Dumontia* is more marked in *Sphaerococcus coronopifolius* (Gigartinales, fig. 154 A), although the ultimate branchlets are cylindrical. The detailed structure ((351) p. 346, (389) p. 47, (634) p. 36)[2] is much like that of *Gloeosiphonia* (fig. 154 C), the flattening being due to the more vigorous development of the laterals arising from two of the four pericentrals; the distichous branches originate from the apical cells of the favoured laterals. The early development is described by Chemin ((129) p. 427). Cf. also *Plocamium* (p. 492).

A similar compression is seen in the stiff cartilaginous fronds of many species of *Gelidium* (especially *G. latifolium* (Grev.) Thur. & Born. ((276) pl. 53, fig. 3) and *Pterocladia*[3] which mostly show repeated

[1] Naegeli's and Dunn's accounts of the apical structure are erroneous. Dunn ((183) p. 435) states incorrectly that a number of threads are involved, although her fig. 11 shows the uniaxial structure quite clearly.

[2] Johnson's description (328) is erroneous.

[3] See (68) p. 57, (196), (205) p. 90, (288), (351) p. 700, (387) p. 25, (494).

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pinnate branching (fig. 155 A). While the apical structure (fig. 155 B) is essentially like that of the genera previously considered, the uniaxial condition is only recognisable in the very youngest parts (cf. fig. 155 C), since the cells produced from the four primary pericentrals soon under-

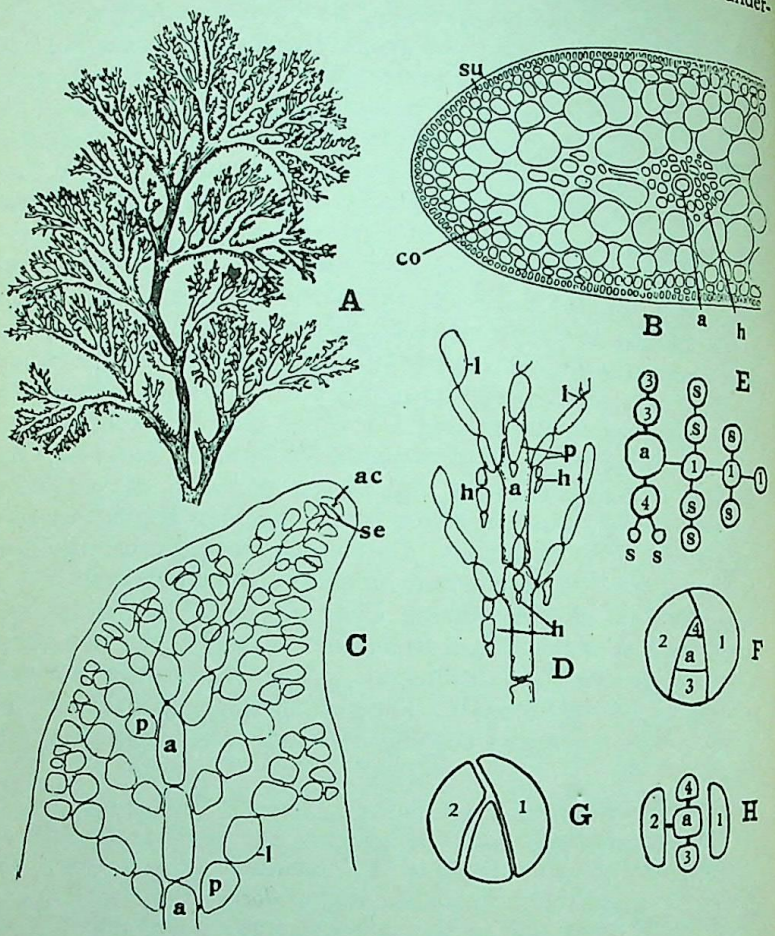

Fig. 154. *Sphaerococcus coronopifolius* C. A. Ag. A, habit; B, transverse section of mature thallus; C, apical cell and segmentation; D, commencement of hypha-formation; E, diagram to show details of branching; F, G, division of primary segments; H, the same, later stage *1–4* successive pericentrals and their products. *a*, axial cells; *ac*, apical cell; *co*, cortex; *h*, hyphae; *l*, laterals; *p*, pericentral (basal) cells; *s*, secondary laterals; *se*, segment; *su*, surface-layer of thallus. (A after Newton; B after Kylin; the remainder after Sjöstedt.)

go pronounced lengthening and form an extensive medulla (*m*). The abundant hyphae (*hy*), most of which have very thick walls, are in *Pterocladia* found only in the medulla, whilst in *Gelidium* they mainly occupy a more peripheral position. The early development ((129) p. 324, (339) p. 260) shows no evident prostrate system (fig. 155 D–G) and the

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growth soon becomes erect. The thalli readily form adventitious branches from wounds ((367) p. 154).

Species of *Gelidium* are found both in the littoral region and in deeper water. The mainly prostrate fronds of the small *G. pusillum* (Stackh.) Le Jol. ((276) pl. 53, fig. 6) are not uncommon near high-tide level, sometimes intermingled with *Catenella Opuntia*; *G. crinale* is important in

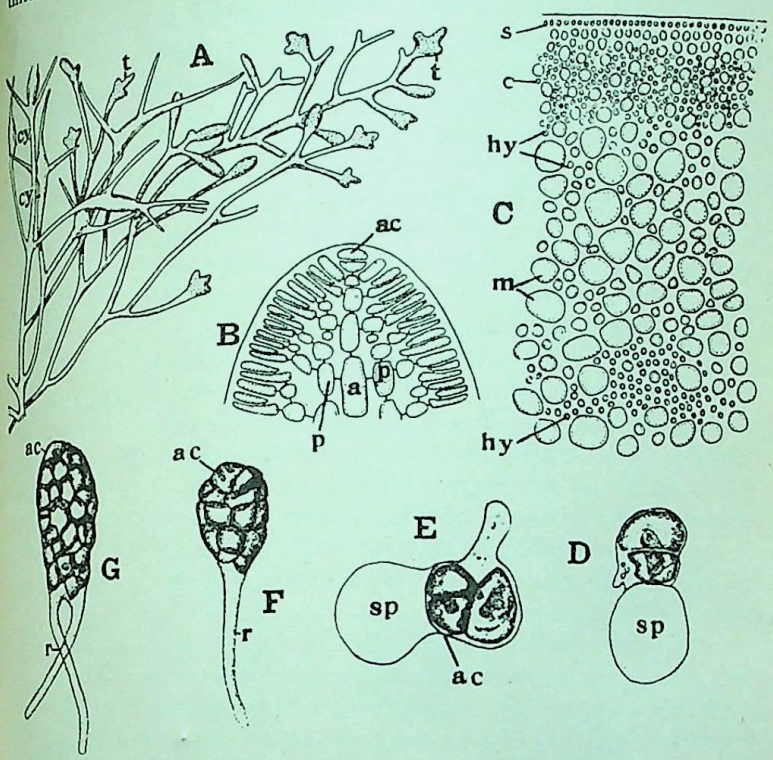

Fig. 155. *Gelidium*. A, *G. crinale* (Turn.) Lamour.; B, C, *G. cartilagineum* Gaill.; D–G, *Pterocladia capillacea* (Gmel.) Born and Thur. A, habit showing cystocarpic (*cy*) and tetrasporic areas (*t*); B, apical cell (*ac*) and segmentation; C, transverse section of mature thallus; D–G, stages in germination. *a*, axial cell; *ac*, apical cell; *c*, cortex; *hy*, hyphae; *m*, medullary cells; *p*, pericentral (basal) cells; *r*, rhizoids; *s*, surface-layer of thallus; *sp*, empty spore-membrane. (A after Taylor; B, C after Kylin; the rest after Killian.)

similar situations in the Mediterranean ((36) p. 408, (226) p. 382) and other warmer seas. The tufts of *Pterocladia capillacea* ((276) pl. 53, fig. 1) are common between tide-levels. *Gelidiella* (*Echinocaulon* Kütz. (196) p. 158, (204) p. 529, (205) pp. 88, 97), with small forms inhabiting warmer seas, has no hyphae.

Although less specialised in its reproduction than most of the genera previously considered, *Lemanea* ((22), (23), (63), (380) p. 5, (502) p. 249,

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(629), (717), (772)) shows marked modification of the ordinary uniaxial type. The species are usually found during the cold season, attached to rocks in water-falls and torrents; they favour siliceous waters (262 p. 52). They are grouped in two subgenera *Eulemanea* and *Sacheria* (23), which show certain differences in structure. The thalli take the form of stiff, olive-green or greenish-black bristles (fig. 156 A), which are simple or branched and normally reach a length of 15–20 cm. Growth is effected by the usual dome-shaped apical cell (fig. 156 I, *s*), but for some little distance behind the apex the axial thread and its whorled branches are little obvious, although evident enough in the maturer parts (fig. 156 H, K, L).

The segments of the apical cell (fig. 156 I, *s*) cut off four pericentrals (*p*), the two first formed (fig. 156 B, *1*) being larger than the others. After this (fig. 156 I) small cells (*u*) are cut off at the upper ends of the pericentrals (*p*), two from each of the larger, but only one from the smaller; in transverse sections therefore either six (fig. 156 D) or four (fig. 156 C) cells are found surrounding the axial cell. All of the peripheral elements subsequently divide horizontally (cf. segments *13–19* in fig. 156 I, J) to produce vertical rows of cells (6 above (*u*) and 4 below (*l*)) which surround the elongating central cell. Each pericentral (fig. 156 E–G, *p*) cuts off successively on its outer side three cells (*c*), and a similar division takes place in each cell of the above-mentioned rows (cf. segment *19* in fig. 156 J). This results in the formation of a small-celled cortical layer (fig. 156 K, *c*) on the outside of a row of more elongate cells (*u*, *l*). By further periclinal division of the peripheral cells (fig. 156 H) the cortical envelope becomes successively 2- to 4-layered.

In the older parts the axial cells (fig. 156 H, K, L, *a*) are separated from the cortex by a space and have undergone great elongation. Just beneath the septa they bear whorls of four laterals (fig. 156 L), the large basal cells (*b*) of which are produced from the inner parts (fig. 156 G, *b*) of the pericentrals; in *Sacheria* (fig. 156 K, *b*) these basal cells are T- or L-shaped, in *Eulemanea* (fig. 156 L, *b*) clavate. It is by their marked radial elongation that the compact superficial tissue of the younger parts is separated from the axial thread. From the outer ends of the basal cells (fig. 156 K, L) arise the ascending (*u*) and descending (*l*) threads (generative filaments of Atkinson), which occupy the inner surface of the wall of the bristle. Their elongate cells are derived from the rows above described. In *Sacheria* they are closely applied to the wall of the bristle, while in *Eulemanea* (fig. 156 L) they are connected with it by oval or pyriform cells (*co*, the tie-cells of Atkinson) which arise at regular intervals. The number of longitudinal threads (6 above and 4 below) remains constant for a considerable distance in *Sacheria*, but in *Eulemanea* branching soon occurs so that there are 8 ascending and 8 descending filaments (122 p. 202).

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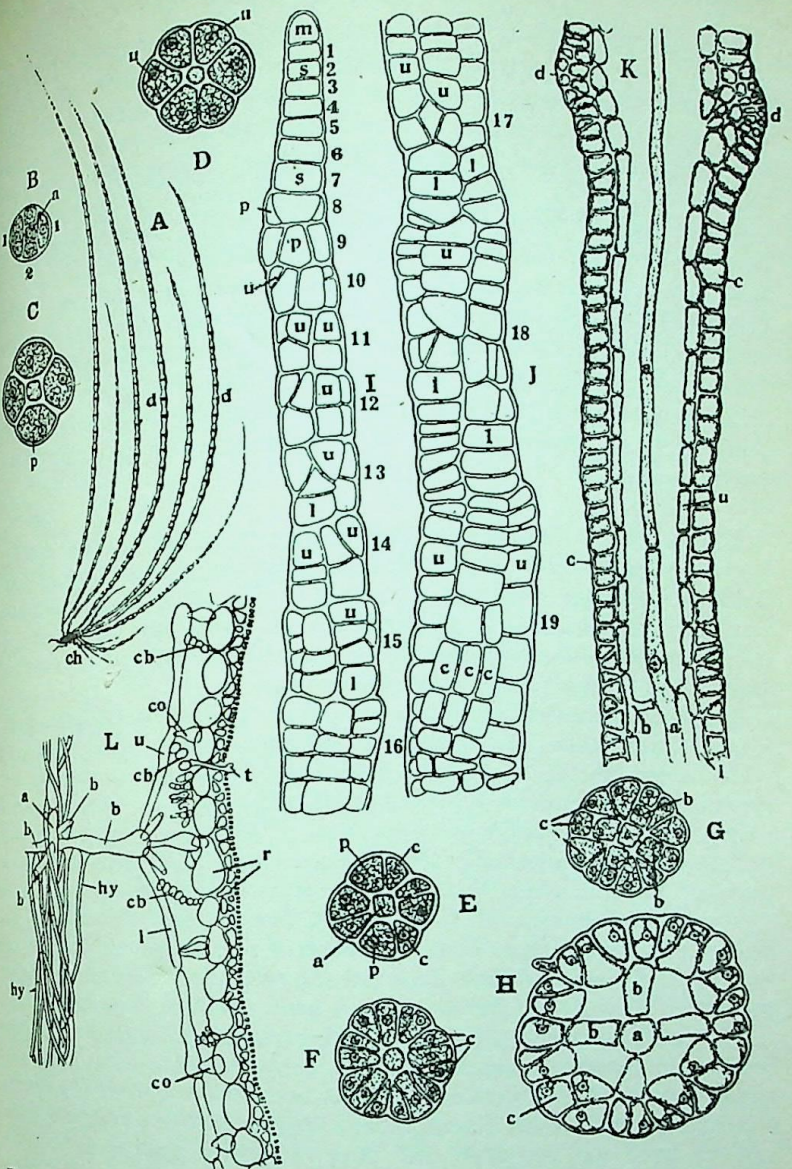

Fig. 156. *Lemanea*. A, *L. nodosa* Kütz. (after Sirodot); B–K, *L.* (*Sacheria*) *fluviatilis* Ag. (after Kylin); L, *L. australis* Atkins (after Atkinson). A, habit; B–H, transverse sections at successively lower levels; I, J, surface-view of the apical part of a bristle, the numerals corresponding to the successive segments; K, longitudinal section through a somewhat older part; L, the same (partly diagrammatic and greatly enlarged) through a mature region, at the level of a primary whorl, with carpogonial branches (*cb*). *a*, axial cells; *b*, basal cells of primary whorls; *c*, cells of primary cortical layer; *ch*, juvenile threads; *co*, tie-cells; *d*, "node" of bristle (point of contact of branch-systems of successive whorls); *hy*, hyphae; *l*, descending longitudinal threads; *m*, apical cell; *p*, pericentral; *r*, cortical cells; *s*, segment; *t*, trichogyne; *u*, ascending longitudinal threads.

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The numerous short branch-systems, arising from the cells of the longitudinal threads and formed by the periclinal divisions above described, constitute the compact 2–4-layered cortex (fig. 156 L, *r*). The outer layer or layers are composed of small cells plentifully supplied with chromatophores. The swellings seen at regular intervals on the bristles (fig. 156 A, K, *d*) mark the points of contact of the ultimate branch-systems of successive whorls (cf. *Gloeosiphonia*) and lie approximately midway between two points of branching of the axial row. Hyphae are found only in *Eulemanea* (fig. 156 L, *hy*), being produced from the proximal ends of the basal cells; they entwine the axial cells and partly fill the central cavity. They usually grow downwards, but in *L. parvula* Sirod. ((629) p. 19) they grow upwards. Branching of the bristles ((22) p. 210) is effected by the outgrowth of a pericentral; the cavity of the branch communicates with that of the parent bristle.

The species of *Sacheria* are often more richly branched and seem to favour more turbulent water than those of *Eulemanea*. To the latter belong *L. annulata* Kütz. and *L. torulosa* Sirod., while *Sacheria* includes such common species as *L. fluviatilis* Ag., *L. fucina* Bory, and *L. mamillosa* Kütz. (regarded by some as a form of *L. fucina*). *L. torulosa* has been found in the littoral flora of lakes (546).

The carpospores of *Lemanea* germinate in the last months of the year, often within the old bristles, and form a juvenile stage (fig. 157 C, G, *ch*) which resembles that of *Batrachospermum*, although apparently less capable of independent existence; it is not known to produce monospores ((22) p. 180, (23) p. 227, (72), (129) p. 320, (512) p. 191, (546), (629) p. 33, (693)). The perennial prostrate system may be filamentous or composed of polygonal cells. In *Sacheria* the erect threads are short, little branched, and ephemeral. The mature bristles arise direct from the prostrate system or from a lateral branch of an erect thread ((629) p. 54; fig. 157 C). They are at first uniseriate (*le*) and only differ from the other threads in their broad flat cells; they soon produce rhizoids (fig. 157 A, *r*). Similar rhizoids emerge from the cells of the juvenile stage and both alike serve to strengthen the attachment and to extend the prostrate system. Their tips may divide to form a secondary prostrate system (fig. 157 A, *d*) so that abundant vegetative propagation is effected and extensive mats are produced. According to Brand ((72) p. 187) cells in the wall of old bristles can also give rise to these juvenile stages. It is manifest that they are directly comparable to those of *Dudresnaya*, *Gloeosiphonia*, etc. (cf. also (247) p. 6).

Tuomeya fluviatilis ((275) p. 64, (599) p. 327, (611)), found in streams in the Eastern United States, appears as rather rigid, richly branched tufts, up to 5 cm. high (fig. 157 F), fixed by a discoid attaching organ. In transverse section (fig. 157 D) the mature parts exhibit much the same structure as in *Lemanea*, the rather narrow cavity around the axial cell (*a*) being filled with plentiful hyphae (*hy*). The apices (fig. 157 B), however, show nothing of the pseudo-parenchymatous structure of

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Lemanea, the developing whorls of laterals (*l*) being plainly recognisable, although behind the apex they become distally compacted to form a continuous surface. In these respects *Tuomeya* is intermediate between *Batrachospermum* and *Lemanea*.

The series of genera considered in this section exhibit a uniform type of apical segmentation, combined with whorled branching. They differ chiefly in the degree of compactness attained, as well as in

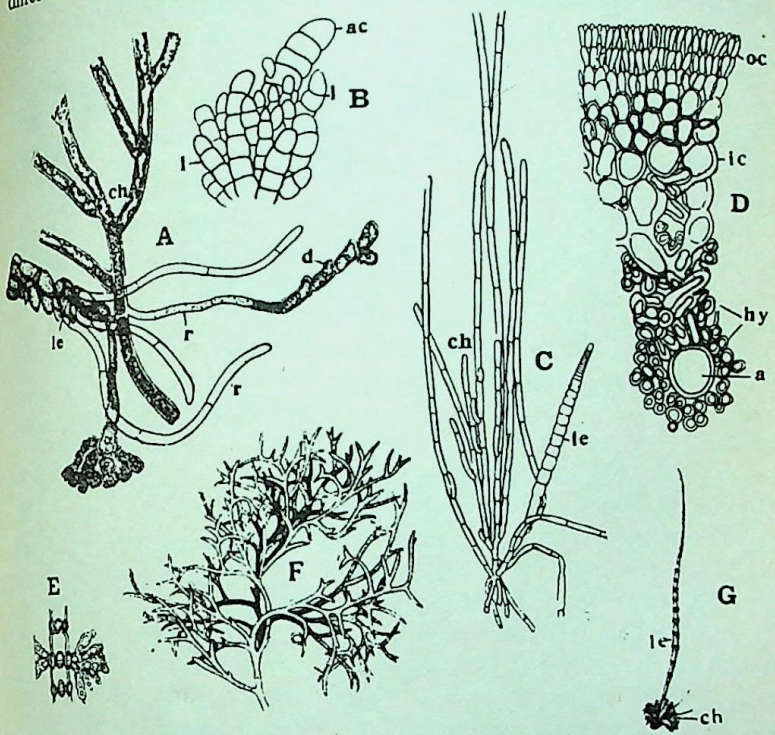

Fig. 157. A, *Lemanea mamillosa* Kütz., base of plant (*le*) arising from juvenile stage (*ch*) showing rhizoids (*r*), in part producing secondary discs (*d*). B, D–F, *Tuomeya fluviatilis* Harv.; B, apex of a growing plant; D, part of a transverse section of a mature thallus; E, small part of thallus (diagrammatic); F, habit. C, *Lemanea annulata* Kütz., juvenile stage (*ch*) with young thallus (*le*) arising as a branch. G, *Lemanea* sp., young plant (*le*) with remains (*ch*) of the juvenile stage at the base. *a*, axial cell; *ac*, apical cell; *hy*, hyphae; *ic*, inner and *oc*, outer cortex; *l*, lateral. (A after Atkinson; C, G after Sirodot; the rest after Setchell.)

minor details of branching, hypha-production, etc. *Lemanea* is distinguished by the parenchymatous structure of the tips, which require detailed study to relate them to the obvious filamentous construction of the maturer parts. In this respect *Lemanea* constitutes a transition from the uniaxial forms with a loose construction to the pseudo-parenchymatous forms dealt with in section 8 (p. 482). It must be

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emphasised, however, that the diverse genera just considered do not constitute a taxonomic series.

6. The simpler Types of Multiaxial Construction and their Elaboration

The species of *Nemalion*, a simple multiaxial type belonging to the same order as *Batrachospermum*, commonly occur between tide-levels and are widely distributed in North Temperate seas, although more

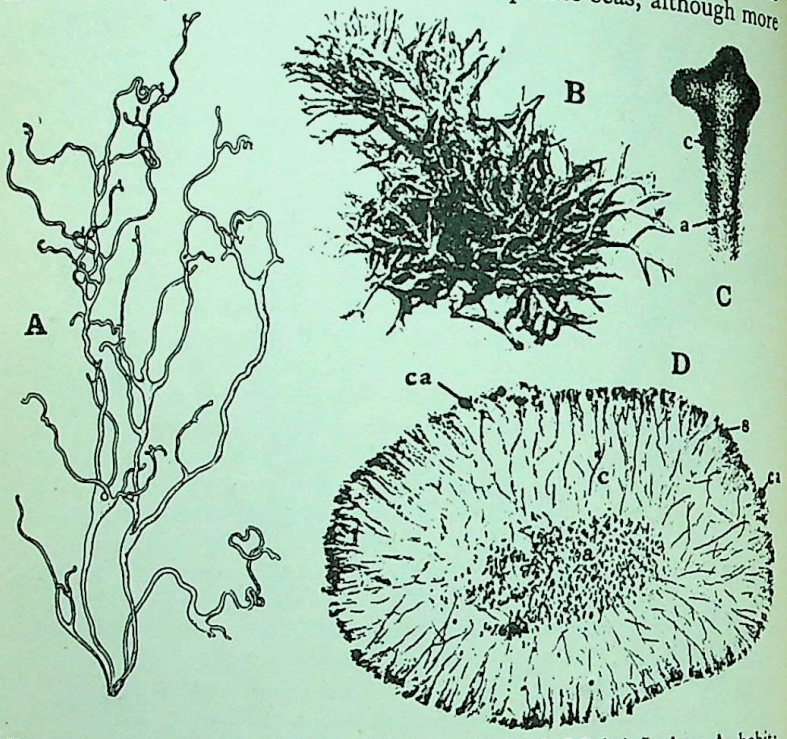

Fig. 158. A, C, D, *Nemalion multifidum* (Web. & Mohr) J. Ag.; A, habit; C, young plant; D, transverse section of mature thallus. B, *Liagora tetrasporifera* Boerges., habit. *a*, axial threads; *c*, cortical region; *ca*, groups of carposporangia; *s*, superficial layer. (A after Taylor; B after Boergesen; C after Rosenvinge; D original.)

frequent in warmer waters. Outwardly the thalli appear as soft gelatinous cylinders reaching a length of 25 cm. and often (e.g. *N. multifidum*; fig. 158 A; (276) pl. 36) showing some dichotomous, as well as lateral branching ((558) p. 144); in *N. helminthoides* (Velley) Batt. ((34) p. 59; *N. lubricum* Duby), however, branching is very limited. The thalli are attached by a discoid base.

The structure ((136) p. 324, (558) p. 144) is readily deciphered by exerting gentle pressure under a cover-glass on the tip of a branch. The threads of the multiple axis, each provided with an apical cell

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devoid of chromatophores, all reach to about the same level (fig. 158 C) and bear numerous richly branched laterals of limited growth (cf. also fig. 159 A). Near the summit these form a radiating group, but farther back they assume a more horizontal disposition and constitute an envelope (*c*) around the axial threads (*a*), the density of which is increased by the intercalation of further laterals. The ultimate branches of the latter reach a uniform level and give the fronds their even surface. In transverse sections of older parts (fig. 158 D) the axial threads (*a*) are separated by a wide space, occupied by mucilage and traversed by the proximal parts of the laterals (*c*), from the more compact cortical region. The narrow elongate axial cells are devoid of chromatophores, but the superficial cells contain a conspicuous stellate chromatophore with a central pyrenoid and usually bear hyaline hairs ((50) p. 62, (136) p. 327, (365), (748) p. 610). The Californian *Cumagloea* ((233) p. 398) shows much the same structure. The dichotomous branching of *N. multifidum* is due to periodical separation of the apical threads into two groups (cf. fig. 159 A).

Essentially the same structure is found in *Platoma Bairdii*[1] ((363), (379) p. 5) in which the thallus is slightly flattened. Here the axial threads protrude, since laterals are only formed a little way below the apex (fig. 159 A). Hyphae arise from their basal cells and give rise to secondary laterals.

The carpospores of *Nemalion* commence to germinate ((131), (136) p. 342, (379) p. 3, (429)) like those of *Batrachospermum* (p. 455), but the protuberance arising from the spore appears to divide horizontally into an upper cell producing an erect thread and a lower one giving rise to the prostrate system. Later stages (cf. also (558) p. 144) are definitely heterotrichous, with a basal system of short rounded cells, bearing well-branched erect threads, and the mature thallus no doubt arises by further development of a group of the latter; the juvenile stage may last for some time before the erect fronds develop ((129) p. 312). In *Platoma* ((363) p. 196) the spores produce a basal crust (fig. 159 D), the erect threads (*e*) of which are closely apposed below and may bear sporangia (*sp*); certain groups of threads sooner or later grow out into erect thalli (*th*).

Diverse other Nemalionales possess a similar, though rather more compact, structure. Examples are furnished by *Liagora* (fig. 158 B, (9) p. 96, (50) p. 66, (320) p. 554, (727) p. 198, (754)) where there is often appreciable calcification, *Trichogloea* ((91), (666) p. 206), the often large *Helminthocladia Calvadosii*[2] ((558) p. 147), and *Helminthora divaricata*[3]

[1] *Nemastoma Bairdii* Farlow ((34) p. 94, (193) p. 142); *Helminthocladia Hudsoni* Batt. non Ag. (33) p. 377). Bornet & Thuret ((68) p. 47) describe the structure of another species (*P. marginifera* (J. Ag.) Schmitz).

[2] *H. purpurea* J. Ag. (cf. (234) p. 212); *Nemalion purpureum* Chauv ((276 pl. 161).

[3] *Dudresnaya divaricata* J. Ag. ((276) pl. 110).

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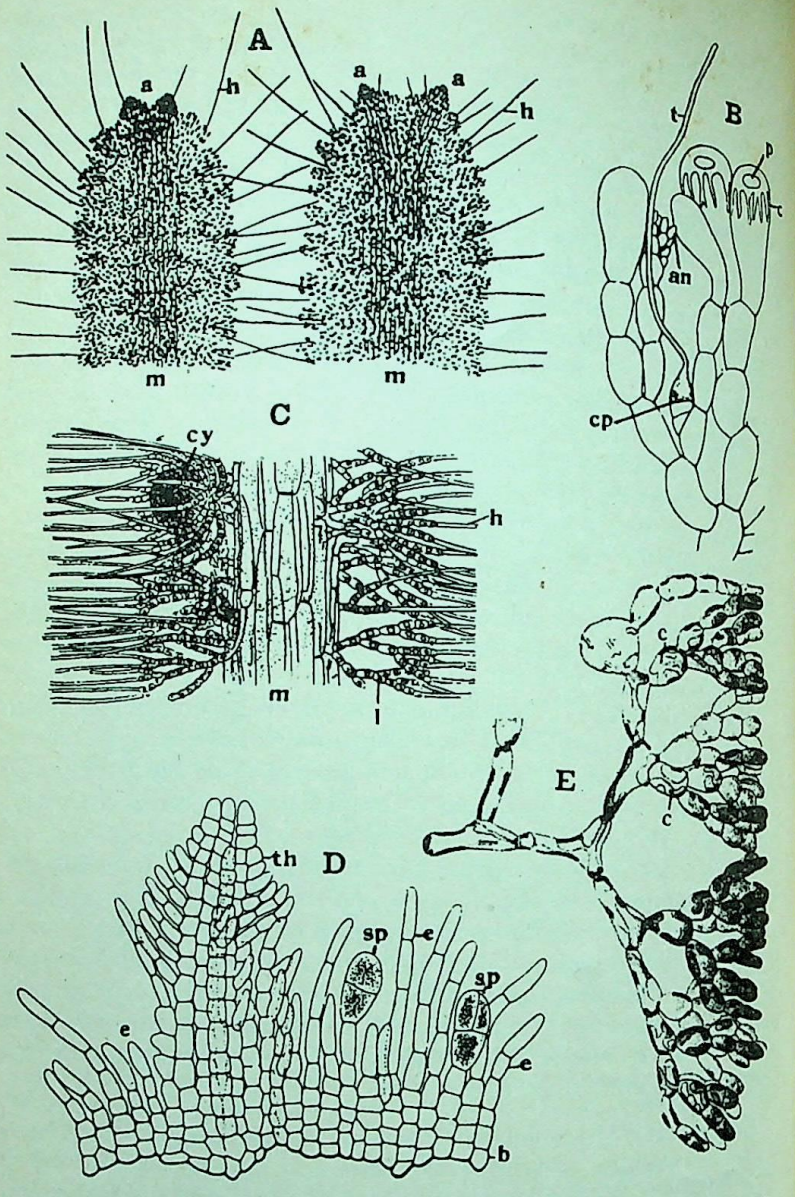

Fig. 159. A, D, E, *Platoma Bairdii* (Farl.) Kuck.; A, diagrammatic representation of the tips of two branches in course of dichotomising; D, juvenile stage, bearing tetrasporangia (*sp*) and a developing thallus (*th*); E, one of the lateral branch-systems. B, *Helminthocladia Calvadosii* (Lamour.) Setch., part of lateral branch-system with sex organs. C, *Helminthora divaricata* J. Ag., -longitudinal section of small part of mature thallus, with cystocarps (*cy*). *a*, apical region of thallus; *an*, antheridia; *b*, basal system of juvenile stage; *c*, chromatophores; *cp*, carpogonium; *e*, erect threads of juvenile stage; *h*, hairs; *l*, lateral; *m*, multiple axis; *p*, pyrenoid; *t*, trichogyne. (B after Rosenvinge; C after Thuret & Bornet; the remainder after Kuckuck.)

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((558) p. 63); the last two are, like *Nemalion*, short-lived summer-forms ((362) p. 445), with plentiful monopodial branching, found near low-water mark. In *Helminthocladia* (cf. also (450) p. 235) the cells of the laterals (fig. 159 B) are appreciably larger than those of the axial threads and increase in size towards the periphery, while in *Helminthora* (fig. 159 C) the axial threads (*m*) are large-celled. Unicellular hairs occur in both ((673) p. 218). The deposition of lime in *Liagora* may be confined to the cortex, but in some species the axial region becomes calcified at some distance from the apex; in this genus there is often considerable production of hyphae.

The germinating spores of *Helminthocladia* and *Helminthora* give rise to a filamentous or discoid prostrate system, the cells of which in the former are stated (106) to contain a number of parietal discoid chromatophores. The mode of origin of the erect thallus is not clearly established, but the prostrate system no doubt gives rise to the discs by which the adult plants are attached.

Somewhat greater specialisation is found in *Scinaia furcellata*[1] (Nemalionales) ((68) p. 18, (202) p. 272, (266) p. 288, (617) p. 92, (671)), widely distributed in the Mediterranean and Northern Atlantic, and for the most part occurring below low-tide level. The gelatinous thalli (fig. 160 A), usually 10–20 cm. in length, are attached by a discoid holdfast and show a compact tufted habit with abundant dichotomous branching. The apices of the axial threads are sunk in a depression (fig. 160 C, *a*) owing to rapid growth of the adjacent laterals. Near the summit the terminal cells (*t*) of the latter are elongate, but farther back many of them enlarge to form a layer of colourless vesicular cells (fig. 160 B, *e*) which contain light-reflecting bodies ((37) p. 697; cf. also p. 585). The photosynthetic cells (*p*) are largely subterminal, although certain narrow terminal ones, which bear hairs (especially on the younger parts) as well as reproductive organs (monosporangia, antheridia, cf. pp. 620, 623), also play a part; these cells may later become vesicular. The chromatophores are devoid of pyrenoids.

The inner cells of the laterals produce downgrowing hyphae which are stated ((617) pp. 86, 92) also to envelop the threads of the axial strand. The early development ((105), (129) p. 360) does not differ essentially from that of other Nemalionales.

The species of *Galaxaura* ((21) p. 32, (50) p. 88, (51) p. 65; (342), (666) p. 212, (682) p. 594, (683), (711), (727) p. 208), found in warmer seas, have a similar structure with the same kind of apical depression, but the cortex is here usually strongly calcified (fig. 161 A), in some species (e.g. *G. corymbifera* Kjellm.) with joint-formation. The end-cells of the laterals contain a campanulate chromatophore with a large central

[1] *Ginnania furcellata* (Turn.) Mont. ((276) pl. 69). Regarding other species, see (617). Some authorities ((105) p. 93, (265) p. 85) regard the deep-water form of Harvey as a species (*S. subcostata* (J. Ag.) Chemin) distinct from the *S. furcellata* found in the lower part of the tidal zone.

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pyrenoid. Asexual and sexual plants often show a striking dimorphism. *Chaetangium* ((599) p. 339), represented by a number of species in Southern seas, shows diverse forms of uncalcified thalli, which are sometimes saccate; the structure is comparable to that of *Scinaia*, but in *C. saccatum* (448) there is no apical depression.

A multiaxial structure, combined with marked calcification, is seen in *Corallina*[1] (Cryptonemiales) ((652) p. 29, (692) p. 94, (758) p. 23). The

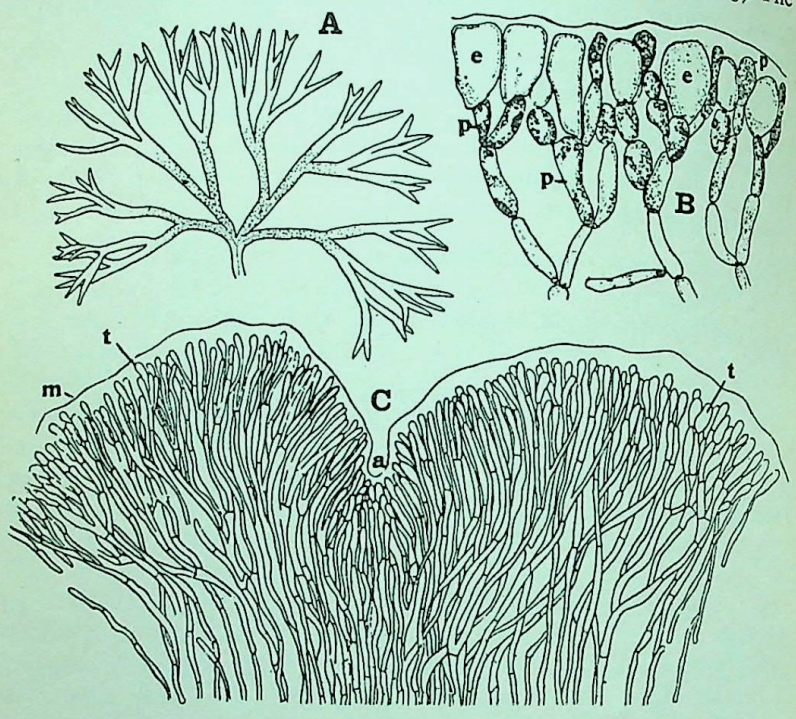

Fig. 160. *Scinaia furcellata* (Turn.) Bivona. A, habit; B, small part showing the ends of the lateral branch-systems; C, apex of thallus. *a*, apical cells; *e*, vesicular "epidermal" cells; *m*, mucilage-envelope; *p*, photosynthetic cells; *t*, tips of lateral threads. (A after Taylor; B and C after Svedelius.)

erect thalli (fig. 161 C, D), composed of numerous calcified segments separated by uncalcified horny and flexible joints, arise from an often extensive basal crust which is commonly lobed. The normal colour is purple or red, although exposed plants are often pink or white as a result of bleaching. *C. officinalis* L. ((276) pl. 222), widely distributed between tide-levels in the Northern Hemisphere, and *C. mediterranea* Aresch., an important constituent of the *Corallina*-girdle situated at about low-tide level on exposed shores in many parts of the Mediterranean ((36) p. 410, (197) p. 202, (226) p. 257), show pinnate branching

[1] For other Corallinaceae, see p. 506.

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so that they present a characteristic feathery habit (fig. 161 C, D); permanently submerged plants are far less plentifully branched. Other species, like *C. rubens*[1] (fig. 161 B), a widely distributed epi-

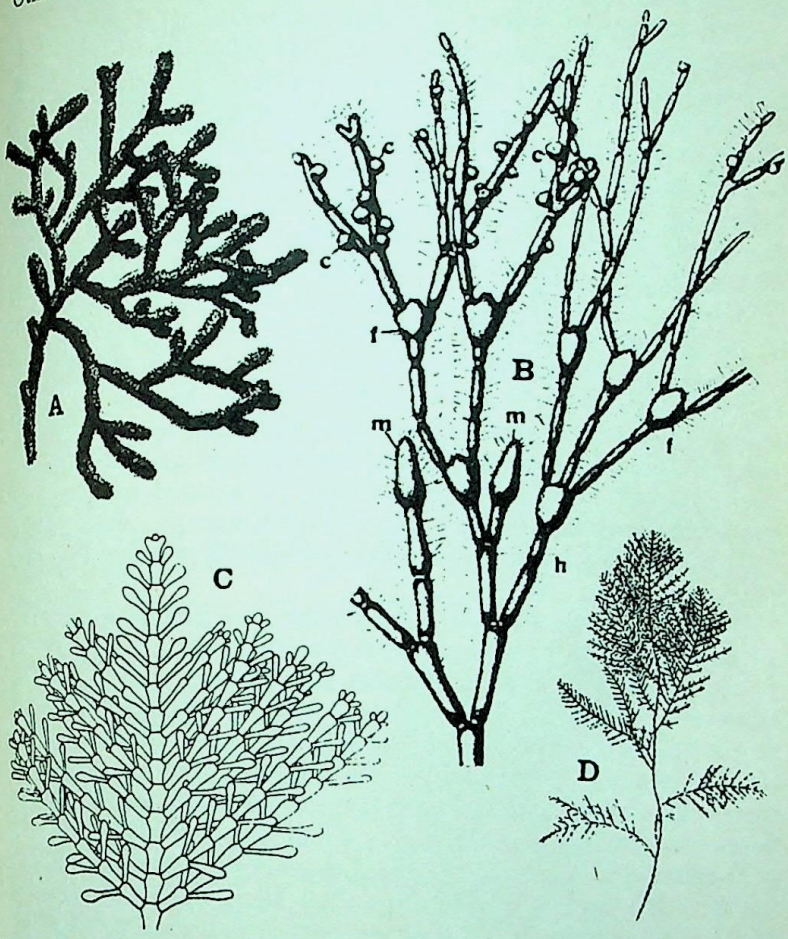

Fig. 161. A, *Galaxaura lapidescens* (Sol.) Lamx. (after Boergesen). B, *Corallina* (*Jania*) *rubens* Ellis & Soland. (after Thuret & Bornet), bearing male (*m*) and female (*f*) conceptacles, as well as conceptacles of the parasitic *Choreonema Thureti* (Born.) Schmitz (*c*); *h*, hairs. C, D, *C. officinalis* L. (after Taylor); C enlarged.

phyte between tide-marks, and *C. pumila* (Lamour.) Kütz. (*Jania pumila* Lamour. (50) p. 191), frequent in warmer seas, show true dichotomy, the successive planes of branching intersecting at various

[1] *Jania rubens* Lamour. ((276) pl. 252). The genus *Jania* is often regarded as a subgenus of *Corallina* (cf. however (50) p. 191, (760) p. 123). *C. rubens* may also show lateral branching ((351) p. 721, (558) p. 275), but according to Suneson ((659) p. 38) this occurs only in the forma *corniculata*.

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angles ((351) p. 707, (659) p. 38). *C. squamata* Ellis ((276) pl. 201), with flattened upper segments, is found near low-water mark. Conspicuous growths of *Corallina* occur between tide-levels in many parts of the world (cf. (227)).

The multiaxial structure is readily recognised after slow decalcification. The axial threads are composed of elongate cells, often arranged in horizontal series (fig. 162 F, L, especially marked in *C. rubens* (558) p. 276) and showing lateral fusions (fig. 162 G, H). Their numerous branches (fig. 162 B, L) bend out gradually to form a compact but not sharply delimited cortex (*c*, very narrow in *C. rubens*, fig. 162 F), the superficial cells of which are markedly flattened (*cover-cells*, *co*, p. 507). In *C. rubens* (fig. 162 F) and certain other species the enlarged end-cells of some of the cortical rows grow out into hairs (*h*), which are not separated from the parent-cell ((659) p. 38). The peripheral cells contain a number of chromatophores.

The apex resembles that of *Nemalion*.[1] Branching (fig. 162 B) is initiated in *C. officinalis* and *C. mediterranea* by the outgrowth of the axial threads (*t*) into usually three apical protuberances (fig. 162 A), the median one (*m*) serving to continue the main axis, while the two lateral ones (*l*) give rise to pinnae; when more than two pinnae are produced, some may develop outside the normal plane of ramification ((558) p. 270). Adventitious branches occasionally originate from older parts.

In the formation of a new segment the axial threads elongate considerably (fig. 162 B) without septation ((558) p. 272, (652) p. 28, (659) p. 30, (759) p. 26), while cytoplasm accumulates at their tips; later these are cut off by transverse septa and divide to form the new segment. The lower portions of the original outgrowing threads do not divide,[2] but with continued lengthening and gradual thickening of their walls develop into the joint (geniculum, fig. 162 A, L, *g*) which bears the new segment above. In *Jania* (fig. 162 F, (724) p. 85) the joint-cells (*g*) are about as long as those composing the axial threads, but in other species of *Corallina* they are appreciably longer (fig. 162 L); they produce little or no cortex and what is formed disorganises at an early stage ((652) p. 28). Since deposition of lime takes place mainly between the cortical threads, the joints remain uncalcified and, although they become more or less overgrown by the cortex of the adjacent segments (fig. 162 L), there is always a gap where the component threads are freely exposed.

The germinating spores ((652) p. 23, (692) p. 100) give rise to a rounded or elliptical disc (fig. 162 C, D) which no doubt develops into

[1] In *C. mediterranea* ((652) p. 31) each apical cell is covered by a thick lamellate wall, slightly impregnated with lime in its outer part, while in *C. rubens* ((652) p. 38) there is only a gelatinous layer over the apex.

[2] Solms-Laubach's statement that they later develop a few transverse walls has not been confirmed by later workers.

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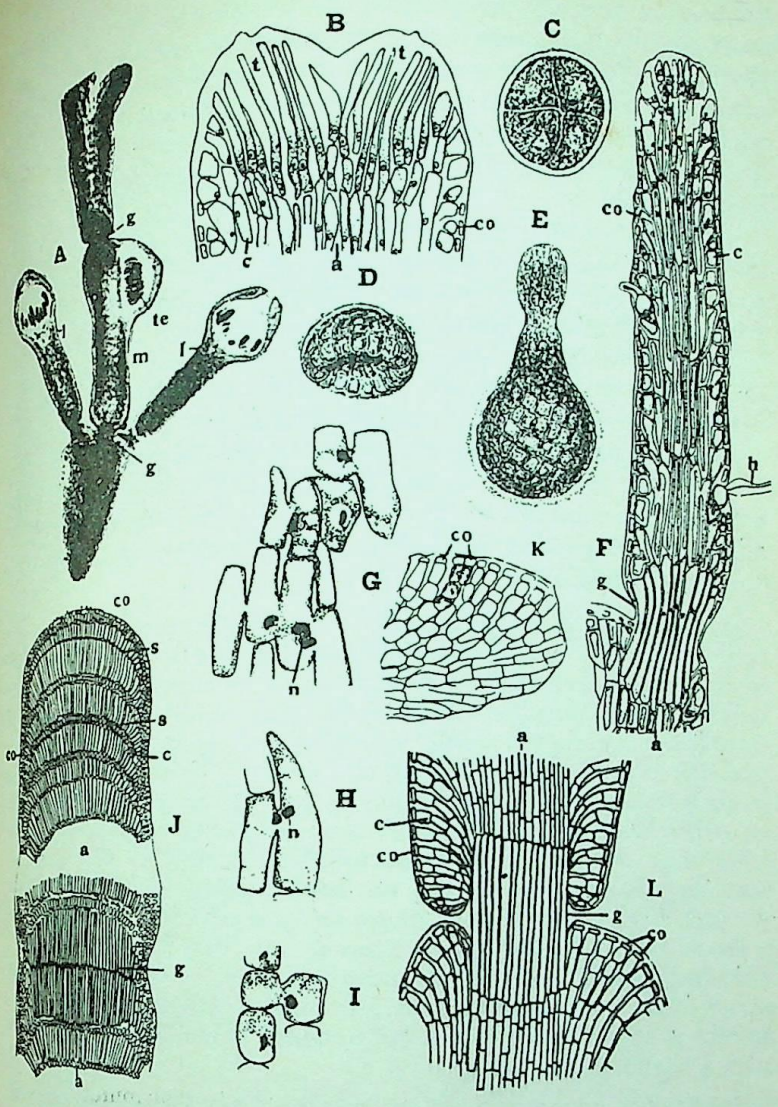

Fig. 162. Corallinaceae. A–I, K, L, *Corallina*; A, L, *Corallina* sp.; B–F, *C. rubens* Ell. & Soland.; G–I, K, *C. officinalis* L. A, longitudinal section of part of thallus with 3 tetrasporic conceptacles (*te*); B, longitudinal section of a dichotomising apex; C–E, successive stages in germination; F, longitudinal section of a terminal segment with the underlying joint (*g*); G–I, cell-fusions; K, edge of basal crust in vertical section; L, longitudinal section through a joint (*g*) and parts of 2 adjacent segments. J, *Amphiroa rigida* Lam., longitudinal section through two segments, with joint (*g*). *a*, axial threads; *c*, cortex; *co*, cover-cells; *g*, joint (geniculum); *h*, hair; *l*, lateral and *m*, main segments; *n*, nuclei; *s* (in J), rows of short axial cells; *t*, tips of outgrowing axial threads; *te*, tetrasporangia. (A, photo: R. Cullen; B, F, J after Suneson; C–E after Thuret & Bornet; G–I, K after Rosenvinge; L, original.)

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the basal crust of the mature plant. In *C. officinalis* ((558) p. 269) this crust (fig. 162 K) consists in its lower part of threads with horizontally elongated cells bearing ascending short-celled filaments, each terminating in a cover-cell (*co*), a structure closely resembling that of the encrusting Melobesieae (p. 508). Several erect shoots usually arise from one and the same crust and a joint is formed at the place of origin of each.

The reproductive organs of *Corallina* are borne in conceptacles (figs. 245 I; 250 C; and p. 644) which, in *C. officinalis* and *C. mediterranea*, occupy the apices of the branches, although the former species also produces lateral conceptacles (fig. 162 A, *te*) which sometimes fuse with one another; according to Solms-Laubach ((652) p. 30) such lateral conceptacles are really formed at the tips of short adventitious branches. In *C. mediterranea* (fig. 250 C) the outer surface of the conceptacles usually bears a considerable number of stiff hairs. In *Jania* (fig. 161 B) new segments arise from the upper corners of the young female conceptacles (*f*) so that the latter are lodged between the uppermost forks of the thallus; the male conceptacles (*m*) are terminal on special branches.

Amphiroa ((652) p. 28, (659) p. 46, (724) p. 79, (758) p. 5), with a similar habit, differs in certain anatomical details (fig. 162 J). The characteristic cover-cells (*co*) extend right over the apex, whereas in *Corallina* they only appear at some distance below it. The elongate cells of the axial threads are interrupted at intervals (*s*) by rows of short ones, a feature which is perhaps related to periodic growth. In certain species the joints consist of two (e.g. *A. rigida*, fig. 162 J, *g*) or several (*A. dilatata*, *A. crassa* Lamx.) rows of cells of about the same length as the other axial ones. Adjacent cells in medulla and cortex are connected by secondary pits ((659) p. 49, (759) pp. 24, 39) like those of *Lithophyllum* (p. 509). The conceptacles of *Amphiroa* occur over the whole surface of a fertile branch. *Cheilosporum* ((724) p. 105, (759) p. 17) differs from *Corallina* mainly in the development from the upper ends of the segments of horn-like outgrowths which usually harbour the conceptacles. Recent workers (cf. (445, 724, 760)) distinguish a number of other genera with a *Corallina*-like habit.

Furcellaria fastigiata ((276) pl. 94), a widely distributed, dark or greenish-purple, perennial lithophyte, belonging to Gigartinales, exemplifies a firmer construction, without accompanying calcification. The rather coarse, dichotomously branched cylindrical thalli, which arise in some numbers (fig. 163 B, E) from a system of branched stolons (*st*) ((98) p. 91, (353) p. 46, (655) p. 400), are often sublittoral, although conspicuous in the lower part of the littoral region on some shores ((633*a*) p. 35).

The structure ((98), (170) p. 9, (502) p. 260, (558) p. 164, (744) p. 86), like that of *Lemanea*, can be readily deciphered only by means of sections, although after suitable treatment (see p. 499) most details

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can be made out by dissection. The apex of the growing thallus (fig. 163 A) is essentially like that of *Nemalion*, but the laterals fit more closely and the whole is enveloped by a firm mucilage-layer (*mu*).

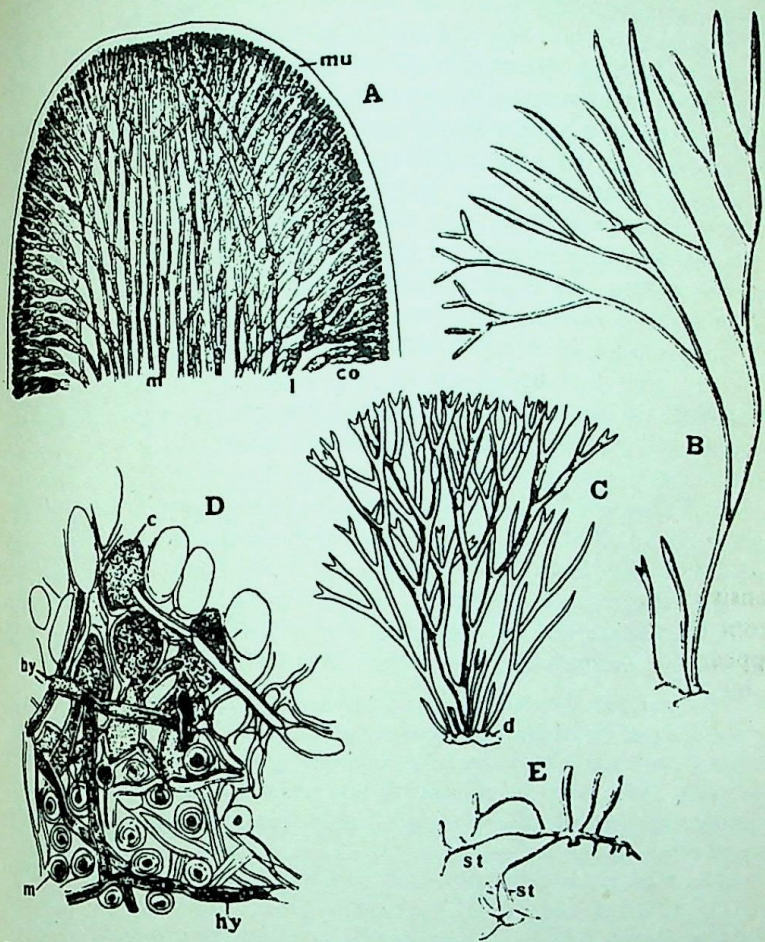

Fig. 163. A, B, D, E, *Furcellaria fastigiata* (Huds.) Lamour.; A, longitudinal section of tip of thallus; B, habit; D, small part of transverse section of a mature thallus; E, basal part of thallus showing stolons (*st*). C, *Polyides rotundus* (Gmel.) Grev., habit. *c*, *co*, cortex; *hy*, hyphae; *m*, cells of central axis; *l*, lateral; *mu*, mucilage-envelope. (A after Oltmanns; B, E after Kolkwitz; C after Newton; D after Rosenvinge.)

Transverse sections through the older parts show a compact structure with considerable differentiation (fig. 163 D). The cells of the axial threads (*m*) have thick stratified membranes and are surrounded by several layers of large cells (*c*), constituted by the basal portions of the laterals and at certain times crowded with starch. The small peripheral

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cells (fig. 163 A, *co*) are provided with plentiful chromatophores. Hyphae (fig. 163 D, *hy*), which aid in the storage of starch during autumn and winter and run mainly in the transverse direction, arise from the inner cortical cells and also ((170) p. 10) from the axial threads; they occur abundantly among the central elements.

The normal branching is stated to be a true dichotomy ((351) p. 348), but there are also adventitious branches ((170) p. 3, (558) p. 166) with a narrow attachment, arising from groups of surface-cells. The tips of the thalli which are crowded with starch ((353) p. 47) become dilated when reproductive organs are formed (fig. 253 C, D). The rest of the thallus persists after these fertile tips are shed and from the scars adventitious shoots may arise which may in their turn become fertile. The germinating spores ((558) p. 170) produce a hemispherical mass of cells giving rise to the cylindrical frond; at an early stage stolons arise from its base and produce other erect fronds.

Very similar in outward habit to *Furcellaria* is *Polyides rotundus* ((276) pl. 95) which belongs to Cryptonemiales. The compact reddish-brown thalli (fig. 163 C) arise in some numbers in each season from a perennial disc (*d*), which may be nearly a centimetre in diameter and has much the same structure (cf. (170) p. 4, (353) p. 51, (363) p. 198) as that of *Dumontia* (p. 461); the older discs are stratified. The thalli show essentially the same structure as those of *Furcellaria* ((98) p. 93, (170) p. 6, (692) p. 75), although the photosynthetic tissue is more extensive and hyphae are fewer. Adventitious shoots frequently arise from the scars left by decay of the thallus-tips. The early stages appear to resemble those of *Furcellaria* ((692) p. 79).

The tropical *Dermonema gracile* (Mart.) Schmitz ((293) p. 289, (681)), a member of Nemalionales, possesses an even firmer texture, the short coarse, repeatedly branched thalli standing erect even when exposed by the tide. This may be related to the presence of a cylinder of thick-walled mechanical cells running longitudinally at the periphery of the loose medulla.

Brief mention may be made of the Grateloupiaceae (Cryptonemiales) ((39) p. 1, (50) p. 122, (58) p. 53, (202) p. 323, (389) p. 19, (634) p. 15) comprising forms with compact thalli in which the medulla consists of widely separated stellate cells (fig. 164 B, C); these owe their distinctive shape to the elongate pit-connections (*p*) which become drawn out during the enlargement of the thallus. There are also more or less numerous, often thick-walled hyphae. *Grateloupia filicina* (fig. 164 A) with a pinnately branched, and *G. dichotoma* J. G. Ag. with a forked thallus, are widely distributed and tend to grow where fresh (and often polluted) water enters the sea. *Cryptonemia* and *Halymenia* are forked leafy forms common in warmer seas. All the contents of the spore pass into a protuberance which divides to form a disc, from which groups of erect fronds arise ((39) p. 5, (129) p. 363, (339) p. 235).

The Mediterranean *Sebdenia Monardiana* (Gigartinales), with a leafy thallus, has a medulla composed of numerous interlacing filaments

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interrupted, especially in the younger parts, by similar stellate cells ((39) p. 4, (251) p. 266, (634) p. 23).

The only fundamental difference between the series of forms described in this and the preceding sections lies in the presence of a single or of a number of axial threads. The early stages are often very similar (cf. *Gloeosiphonia*, fig. 153 C and *Platoma*, fig. 159 D) and the underlying heterotrichy is obvious in all the less specialised types. In tracing the further elaboration of the Floridean thallus, some reference must first be made to certain more specialised uniaxial types among Nemalionales in which the whorled branching characteristic of the more primitive forms is obscured.

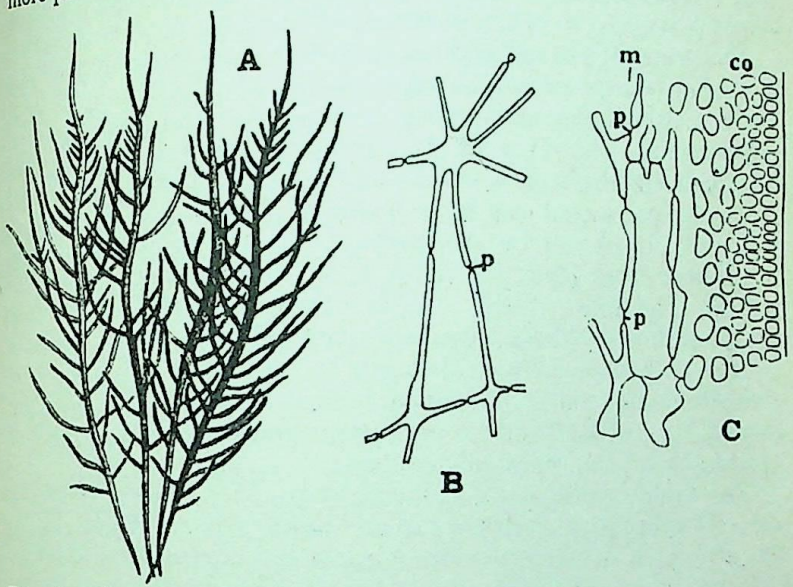

Fig. 164. *Grateloupia filicina* (Wulf.) Ag. A, habit; B, cells of medulla; C, longitudinal section of small part of thallus. *co*, cortex; *m*, medulla; *p*, pit-connections. (A after Kützing; B, C after Kylin.)

7. Specialised Uniaxial Types among Nemalionales

Naccaria Wigghii ((68) p. 52, (147), (276) pl. 38, (387) p. 15, (766) p. 387), in habit much like *Atractophora* (p. 457) and belonging to the same family, has an apical cell (fig. 165 A, *m*) which divides by oblique walls so that the segments (*s*) appear wedge-shaped, the wider part being orientated successively in four different directions. Each segment forms only two pericentrals (fig. 165 B); the first (*a*) is cut off near the apex on the higher side (acroscopic), the second (*b*) only at some slight distance from the apex at the lower end (basiscopic) of the elongating segment and in a plane perpendicular to the other. The respective pericentrals produce primary (*pl*) and secondary (*sl*)

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laterals of limited growth, the former being longer and more richly branched than the latter; the secondary lateral of a given segment is only slightly above the primary one of the segment below and stands almost opposite to it. The laterals are thus arranged in four vertical rows. Hyphae (*hy*) originate as usual from the basal cells, and in the younger parts bear short photosynthetic threads which subsequently fall off. The hyphae give rise both to the small-celled surface-layer and the large-celled cortex which surround the narrow axial cells in the mature thallus, whose increase in thickness is due to branching of the hyphae. Branches of unlimited growth (fig. 165 B, *br*) arise from the basal cells (cf. *Batrachospermum*) of certain primary laterals, but they can also develop adventitiously from the cortical cells. The early stages ((108), (129) p. 316) are essentially like those of *Atractophora*.

The same type of apical division, with formation of only two (here opposite) laterals from each segment (fig. 165 D, J), is seen in the Bonnemaisoniaceae, comprising *Asparagopsis* and *Bonnemaisonia*. *Asparagopsis*, which has its chief centre in warmer seas and in the Southern Hemisphere, is represented in Europe by *A. armata* Harv. ((277) pl. 192) introduced from Australia (cf. (195) p. 791, (569) p. 8, (679) p. 7, (738)) and by *A. hamifera*[1] (fig. 165 E; (492) pls. 183–4) introduced from Japan (cf. (30) p. 9, (88), (121), (142) p. 136, (311), (567) p. 22). The rather small, well-branched, erect fronds arise from creeping shoots which are probably perennial; they are distinguished by the possession of vesicular cells (p. 587), also characteristic of *Bonnemaisonia*, and of modified branches which act as attaching organs (fig. 165 E, *t*) and aid in vegetative propagation (p. 588). Both species have been repeatedly studied.[2]

The higher sides of the segments lie on a 1/4 spiral in *A. armata*, on a 3/8 spiral in *A. hamifera* and give rise to primary laterals (fig. 165 D, *pl*) which develop into unbranched sterile structures of limited growth. A few of the secondary laterals (*sl*), cut off opposite to the primary ones, grow out into long shoots, but most remain short and bear the reproductive organs; both kinds are branched, forming primary and secondary laterals like the parent axis. The first (adaxial) primary lateral of a short shoot grows very rapidly and overarches the latter so that the short shoot appears to arise from the base of the lateral.

In *Bonnemaisonia asparagoides*[3] ((276) pl. 51), an annual lithophyte usually found submerged, the main axes bear progressively weaker laterals which are pinnately branched to the second degree. The wedge-shaped segments of the apical cell (fig. 165 J) are orientated

[1] *Bonnemaisonia hamifera* Hariot (cf. however (208)).

[2] See (121), (141) p. 136, (200), (265) p. 105, (387) p. 23, (679) p. 7; regarding *A. taxiformis* (Delile) Collins & Hervey (*A. Delilei* Mont.; *Dasya Delilei* Mont.), see (21) p. 47, (50) p. 352.

[3] See (145) p. 52, (372), (376) p. 546, (558) p. 401, (744) p. 73.

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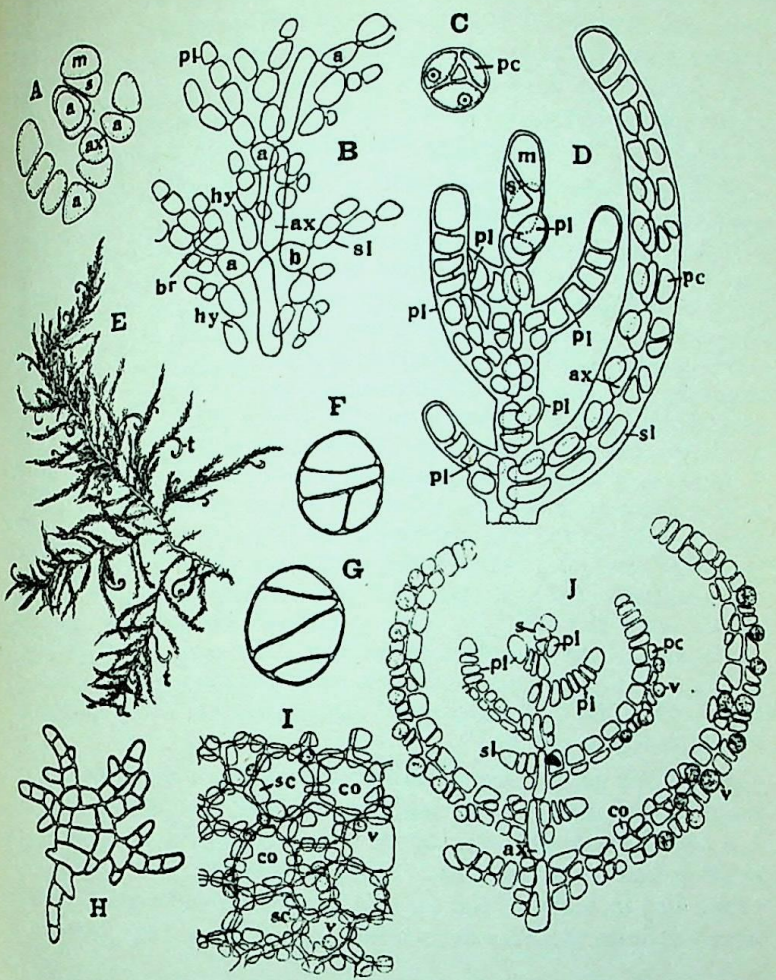

Fig. 165. A, B, *Naccaria Wigghii* (Turn.) Endl.; A, apex of a thallus-branch; B, production of laterals, etc. behind apex. C, F–J, *Bonnemaisonia asparagoides* (Woodw.) Ag.; C, transverse section of a primary lateral just behind the apex; F, G, segmentation of spore; H, juvenile stage; I, surface-view of cortex (*co*) of a primary lateral; J, apex of a branch showing method of segmentation and the formation of the cortex on the primary laterals (*pl*). D, E, *Asparagopsis hamifera* (Hariot) Okam.; D, apex of a thallus-branch; E, habit. *a* (in A and B), first and *b* (in B) second pericentral; *ax*, axial cells; *br*, branch; *co* (in I and J), primary cortical cells; *hy*, hyphae; *m*, apical cell; *pc* (in C and J), pericentral cells; *pl*, primary laterals; *s*, segments of apical cell; *sc*, secondary cortex; *sl*, secondary laterals; *t*, tendrils; *v*, vesicular cells. (E after Taylor; the rest after Kylin.)

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in two opposite directions and all the branching is distichous. The primary (*pl*) and secondary (*sl*) laterals develop as in *Asparagopsis*. In both genera (see (141) p. 140, (387) p. 24) they develop a cortex which arises in a different manner on the primary and secondary laterals. The cortex may be of considerable thickness on the older axes of *Asparagopsis* and is separated by a space, occupied by hyphae in *A. taxiformis* (cf. (50) p. 354), from the elongate axial cells.

In *Bonnemaisonia* the segments of the primary laterals (fig. 165 C) divide into a small central and three pericentral cells (*pc*), the first of which is situated on the abaxial side (fig. 165 J, *pc*) and forms a vesicular cell (*v*) at its upper end. After this each pericentral cuts off four primary cortical elements (*co*), any one of which may divide with the formation of further vesicular cells. As the axial cells elongate, the primary cortical elements form a compact large-celled layer around them (fig. 165 I, *co*) and by degrees the cells of this envelope cut off a considerable number of small cells (*sc*) which overlie the septa between the large ones and in part become vesicular cells (*v*).

In the long shoots, that develop from the secondary laterals, the first four or five segments of the apical cell are cut off transversely and these form a cortex in the way just described. That of the later segments, on the other hand, originates by the cutting off of three pericentrals from the basal cells of the laterals; each pericentral cuts off four cells which divide again and again to form a compact two-layered cortex. The fertile shoots are described on p. 617. The early development ((120) p. 322, (251) p. 261, (379) p. 12) results in the formation of a basal disc (fig. 165 H), the first divisions of the carpospores being vertical to the substratum (fig. 165 F, G).

The three genera just described are clearly more specialised than other Nemalionales. They demonstrate that, even in this order, there has been considerable vegetative advance and this is also evident in their reproduction (p. 616). Oblique division of the apical cell is found also in many of the uniaxial Cryptonemiales and Gigartinales where definite two- or three-sided apical cells are encountered.

8. The more specialised Uni- and Multiaxial Types among Cryptonemiales and Gigartinales

Although the basic mode of construction remains the same, many members of these two orders afford evidence of specialisation in one direction or another. In several the uniaxial structure becomes obscured in the mature thallus. These features may be illustrated by the description of selected examples which have been fully studied.

(*a*) *Uniaxial Forms*

A definite two-sided apical cell is found in diverse Cryptonemiales, such as *Cryptosiphonia* (Dumontiaceae; (389) p. 23, (634) p. 4; fig. 166 A, *a*), *Endocladia* ((387) p. 41, (716); fig. 166 C, *a*) and *Gloeopeltis*

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(Endocladiaceae, (389) p. 17, (463), (634) p. 9), all three mainly found in the Pacific. The species of *Endocladia* and *Gloeopeltis* (*G. capillaris*, *G. furcata*) tend to occur near high-tide level ((227), (467) p. 64, (623) p. 296), the latter especially being capable of withstanding consider-

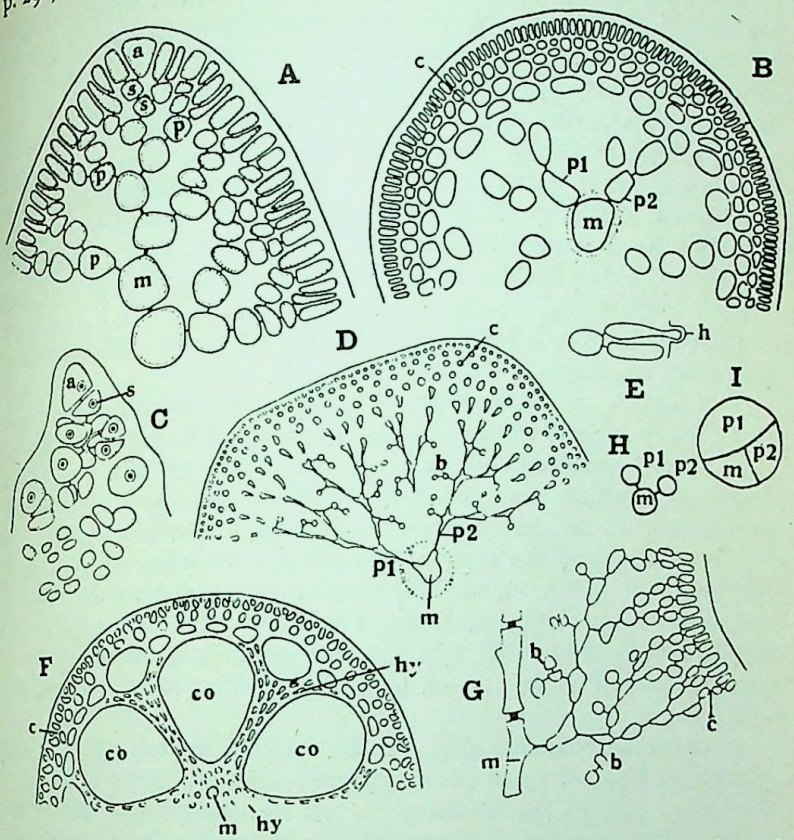

Fig. 166. A, B, *Cryptosiphonia Woodii* J. Ag.; A, longitudinal section through apex; B, transverse section. C–E, G, *Endocladia muricata* (Post. & Rupr.) J. Ag.; C, apex of thallus; D, transverse section; E, developing hair (*h*); G, part of longitudinal section of a young branch. F, *Mychodea ramulosa* J. Ag., transverse section. H, I, *Gloeopeltis furcata* (Post. & Rupr.) J. Ag.; H, diagram to show pericentral formation just behind apex; I, division of primary segment. *a*, apical cell; *b* (in D, G), accessory branchlets; *c*, cortex; *co*, large cells of inner cortex; *hy*, hyphae; *m*, axial cells; *p*, *p1*, *p2*, pericentrals; *s*, segments of apical cell. (H and I after Sjöstedt; the rest after Kylin.)

able desiccation (468). The usually terete well-branched thalli show little differentiation. The segments (fig. 166 A, C, *s*) of the apical cell (*a*) cut off two pericentrals (*p*) in the same way as in *Cystoclonium* (cf. below and fig. 166 B, D, H, I, *p1*, *p2*), and these develop into laterals which form a compact cortex (fig. 166 B, D, G, *c*). It is characteristic of the Endocladiaceae (fig. 166 D, G) that, at each point

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of ramification of the laterals, only two branches are formed, while *Endocladia* itself is distinguished by the numerous accessory branchlets (*b* in fig. 166 D, G) arising from the inner cells. The inner cortex of *Gloeopeltis* is traversed by numerous hyphae.

Cystoclonium purpureum (*C. purpurascens* (Huds.) Kütz.)[1] (Gigartinales) shows a greater degree of internal differentiation. It is a not uncommon lithophyte between tide-marks in Britain, although elsewhere frequently growing submerged. The terete, somewhat cartilaginous thallus (fig. 168 C), which is often dull purple in colour and may reach a length of 60 cm., has a prominent main axis bearing numerous richly branched laterals. Certain branches may end in tendrils (p. 588). The plants are primarily anchored by a minute disc, but the base of the axis later gives rise (fig. 168 C, D) to a number of stolons (*st*) which become attached by squat haptera (*h*) and produce further erect shoots ((291) p. 374, (558) pp. 590, 593, (655) p. 400). The individuals commonly last for one season only, although some perennate by means of the stolons ((291) p. 376).

The anatomical structure has been repeatedly examined ((291), (380) p. 23, (475) p. 241, (489)[2], (558) p. 589, (742) p. 17). The segments (fig. 167 A, *s*) of the two-sided apical cell (*a*) cut off two pericentrals on their higher side which is situated alternately to right and left; the two pericentrals lie in perpendicular planes (cf. *Naccaria* and fig. 166 H, I). The rest of the segment constitutes the axial cell (*m*). Such asymmetrical development of pericentrals takes place in many of the more specialised Florideae. The axial cells undergo marked elongation (fig. 167 C, *m*), while the pericentrals as usual give rise to richly branched laterals which form the compact cortical region (fig. 167 B, C, *co*).

In the older branches (fig. 167 B, C) one can recognise a single superficial layer of small photosynthetic cells (*e*), many of which in the earlier part of the season grow out into long hairs, and several layers of large multinucleate thick-walled storage-cells (*co*, cf. fig. 139 L; (380) p. 24, (742) p. 32). At an early stage the axial thread (fig. 167 D, H, *m*) becomes surrounded by accessory longitudinal threads (*t*), from which it is only distinguished by the greater length of its cells; the entire complex constitutes a probable conducting system (medulla, fig. 167 B, *me*), the transverse septa of which are stated ((742) p. 76) to be perforated by fine cytoplasmic strands. The accessory threads are partly formed by elongation of the inner cells of the laterals and partly by outgrowths from the latter, as well as from the cortical cells. The latter, as well as those forming the conducting tissues, are connected both *inter se* and with one another by means of short hyphae (fig. 167 D–H, *hy*) which develop secondary pit-

[1] *Hypnea purpurascens* ((276) pl. 116); *Gracilaria purpurascens* Naegeli ((475) p. 241).

[2] This refers to *C. armatum*, a species with a wide range in Japan.

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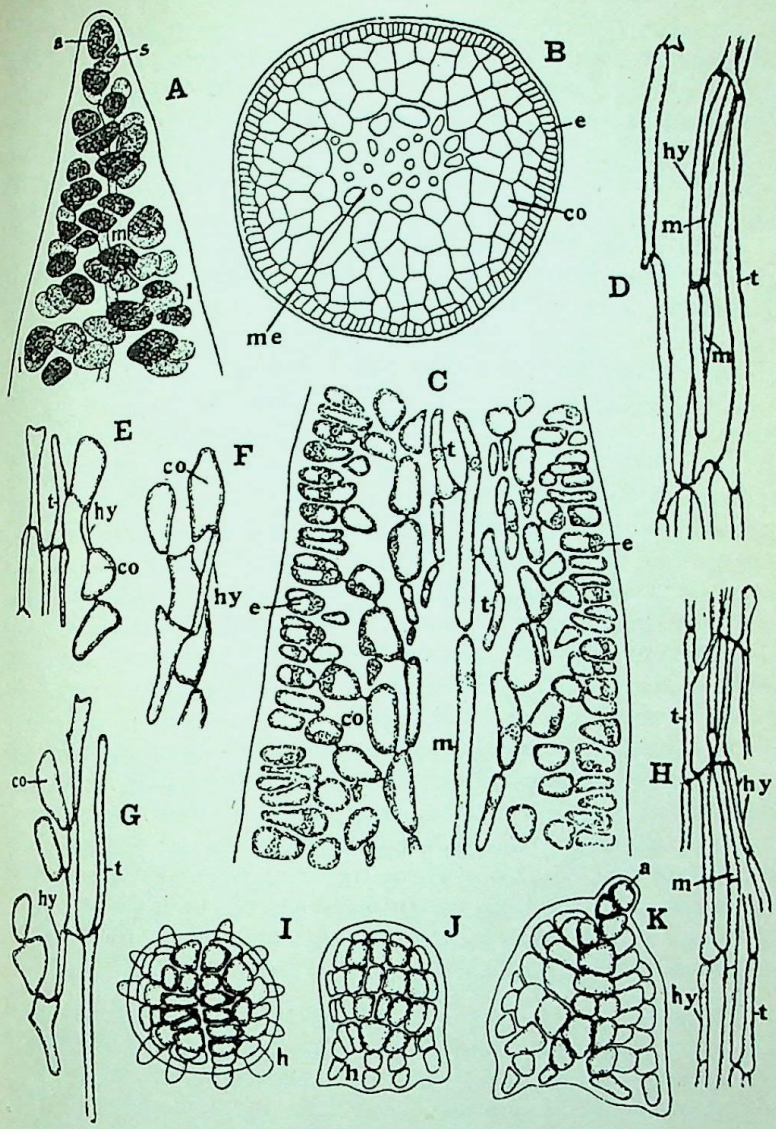

Fig. 167. *Cystoclonium purpureum* (Huds.) Batt. A, apex of a thallus-branch apical cell and segmentation; B, transverse section of a mature branch C, longitudinal section of same; D, H, elements from the medullary region E–G, elements from the cortical region; I–K, early development, I from above, J, K from the side. *a*, apical cell; *co*, cortex; *e*, surface-layer of thallus *h*, haptera; *hy*, hyphae; *l*, lateral; *m*, axial cells; *me*, medulla; *s*, segment o apical cell; *t*, longitudinal threads around axial thread. (All after Kylin.)

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connections at their tips. A branch of the thallus can arise from any peripheral cell.

The spores ((129) p. 431, (379) p. 7, (558) p. 592) undergo vertical or irregular division to form the primary hemispherical attachment-disc (cf. *Dumontia*, *Furcellaria*), which is scarcely larger than the spore and is anchored by short unicellular haptera (fig. 167 I, J). A superficial cell (fig. 167 K, *a*), not always at the summit of the disc, becomes the apical cell of the thallus; sometimes two erect fronds develop from one disc.

A similar apical structure and mode of segmentation is found in other Gigartinales, for instance in the Australian *Erythroclonium*, in *Catenella* ((387) p. 65, (527) p. 65), and in *Hypnea*. The thallus of the first ((141) p. 156) is terete and moniliform (fig. 168 B). *Catenella Opuntia* ((276) pl. 88; *C. repens* Batt.), widely distributed near high-water mark and also occurring commonly in salt-marshes ((96) p. 352, (97) p. 207, (101) p. 191, (142) p. 82), is a perenniai alga in which the small thalli (fig. 168 E) show frequent constrictions. Diverse species of *Catenella* (incl. *C. Opuntia* ((48) p. 45) are characteristic components of the algal vegetation found on the roots of Mangroves, to which they are attached by haptera (*h*) (see (50) p. 359). *C. Nipae* Zanard. is used as a food in Burma (61, 528). The anatomical structure of *Catenella* ((281) p. 71, (387) p. 65) resembles that of *Cystoclonium*, but there are several layers of photosynthetic cells and the inner branches of the laterals are often widely separated. The thick-walled elements of the medulla are linked by secondary pit-connections.

Hypnea musciformis (fig. 168 A), which is common in warmer seas and found elsewhere only in sheltered habitats ((685) p. 291), has fleshy terete thalli, up to 45 cm. long, with numerous short branches; many of the longer ones (*t*) are incurled at the tip and function as tendrils (p. 588). The mature structure ((389) p. 50) differs from that of *Cystoclonium* in the uniform enlargement of the inner cells of the laterals so that the axial cells remain clearly evident. Hairs are often abundant in well illuminated situations ((50) p. 382).

The same apical segmentation is also seen in the Australian genus *Mychodea* (Gigartinales (277) pl. 142, 201, (393) p. 62), with a flattened or foliaceous thallus. The narrow axial cells (fig. 166 F, *m*) are difficult to distinguish in the mature thallus from the numerous surrounding hyphae (*hy*), which also occur between the huge cells (*co*) forming the inner cortex.

A different structure is found in *Gracilaria*, of which *G. confervoides* ((276) pl. 65) is a widely distributed northern lithophyte found at low-tide level and below, although a characteristic inhabitant of sandy bottom in the Mediterranean ((36) p. 432, (226) p. 271). Its dark-red terete fronds, which are up to 50 cm. long, bear more or less numerous tapering branches (fig. 170 B) and several arise from a large

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fleshy disc composed of closely compacted vertical threads ((558) p. 602); this, as well as the greater part of the erect thallus, persists from one season to the next. Other species have more or less com-

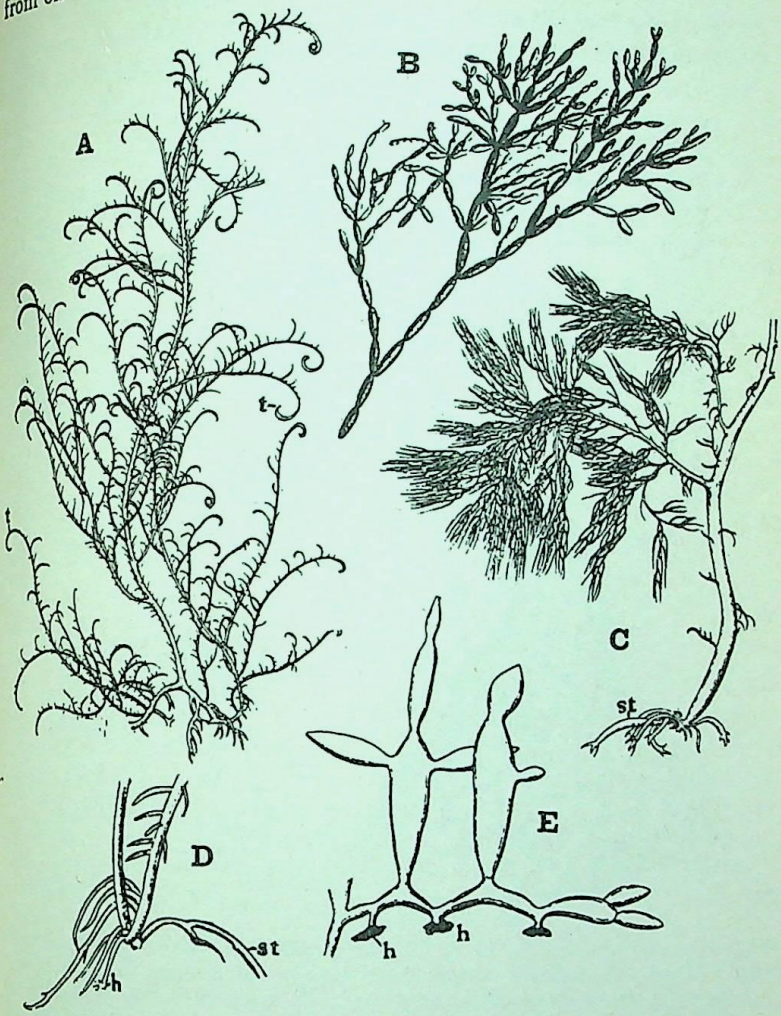

Fig. 168. A, *Hypnea musciformis* (Wulf.) Lamour., habit. B, *Erythroclonium Müller*i Sond., habit. C, D, *Cystoclonium purpureum* (Huds.) Batt.; C, habit; D, base of thallus with stolons (*st*). E, *Catenella Opuntia* (G. & W.) Grev., habit. *h*, haptera; *st*, stolons; *t*, tendrils. (A, C after Taylor; B after Kützing; D after Rosenvinge; E after Boergesen.)

pressed thalli (e.g. *G. multipartita* J. Ag.[1] (276) pl. 15). The spores ((339) pp. 254, 271, (692) p. 83) divide to form a circular disc, the centre of which gradually becomes arched (fig. 169 C), the three-sided apical

[1] *G. lacinulata* (Vahl) Howe ((50) p. 379, (53) p. 83).

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cell (*a*) of the future thallus differentiating at the summit of the arch. Kylin ((389) p. 55; cf. also (191) p. 176) has demonstrated a similar apical cell in the adult fronds (fig. 169 D), although others ((523) p. 788, (634) p. 53) have described a group of apical cells.

The mature thallus ((389) p. 55, (558) p. 603, (634) p. 53, (692) p. 81) shows little anatomical differentiation (fig. 169 A, E), since all the

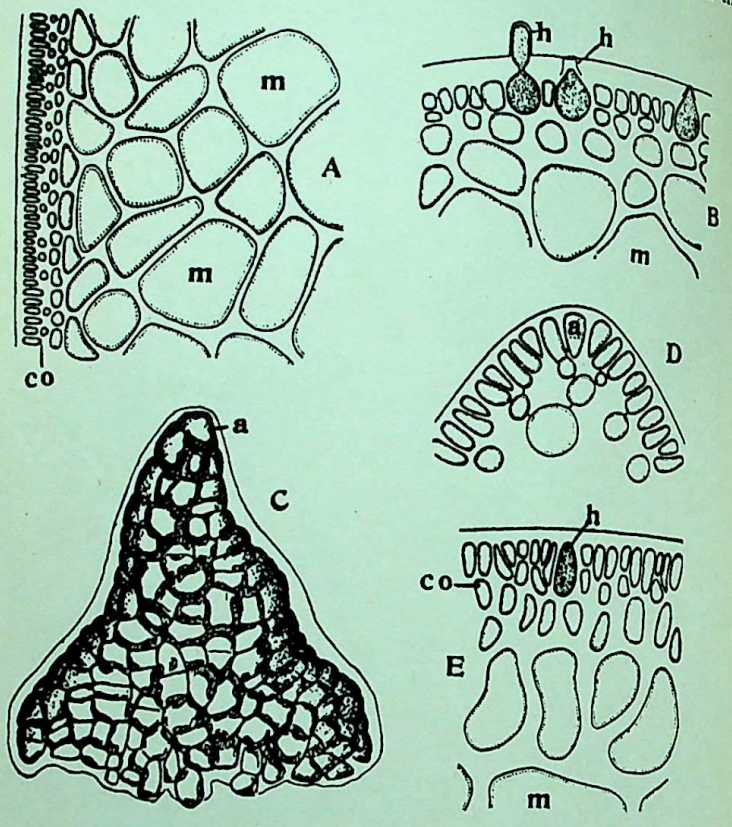

Fig. 169. *Gracilaria*; A, C–E, *G. confervoides* (L.) Grev.; B, *G. compressa* (Ag.) Grun. A, part of longitudinal section of thallus; B, E, transverse sections; C, early stage of development; D, apex of thallus in longitudinal section. *a*, apical cell; *co*, cortex; *h*, hairs and hair-producing cells; *m*, medulla. (C after Killian; the remainder after Kylin.)

internal cells (*m*) are large and isodiametric and an axial thread is unrecognisable. The small cells forming the narrow cortical zone contain a number of ribbon-shaped chromatophores. Unicellular hairs arise from enlarged peripheral cells (fig. 169 B, E, *h*) which possess abundant contents and later become multinucleate.

The instances hitherto considered in this section show how, despite an essentially similar apical structure, the primary uniaxial

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construction may become obscured among Gigartinales, either by the development of accessory longitudinal threads (*Cystoclonium*, *Catenella*) or by equal enlargement of all the internal cells (*Gracilaria*). Other uniaxial Gigartinales show marked flattening of the thallus.

A good example is furnished by *Rhodophyllis bifida* (*Rhodymenia bifida* Grev. (276) pl. 32), a sublittoral form with a repeatedly forked bright red thallus (fig. 170 C) belonging to the same family as *Cysto-*

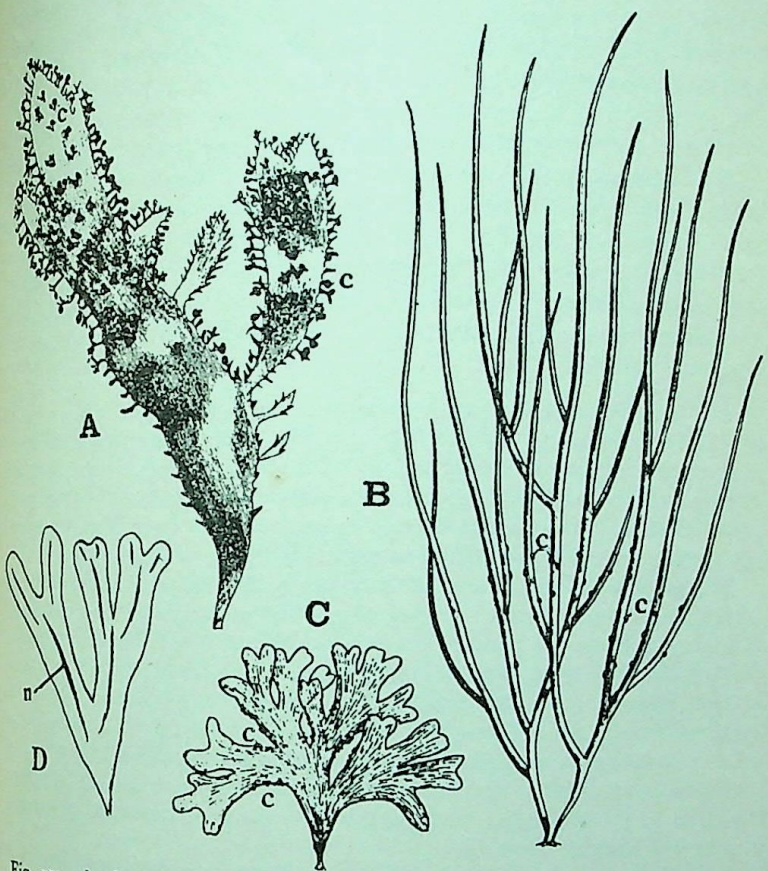

Fig. 170. A, *Calliblepharis ciliata* Kütz., with cystocarps (*c*). B, *Gracilaria confervoides* (L.) Grev., with cystocarps (*c*). C, *Rhodophyllis bifida* (G. & W.) Kütz., with cystocarps (*c*). D, *Stenogramma interrupta* Mont., with nemathecia (*n*). (A after Kützing; B, C after Newton; D after Harvey.)

clonium. According to Kylin ((380) p. 31, (393) p. 40; cf. also (339) p. 249, (351) p. 700, (537) p. 119) the young fronds possess a two-sided apical cell (fig. 171 A, *a*), the segments of which divide periclinally into outer (*o*) and inner (*i*) cells. The outer undergo further periclinal division, but some soon enlarge (*sa*) and divide obliquely to constitute

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secondary apical cells (*a1*, *a2*) which continue to segment in the same manner. In older plants, in which the tips of the fronds have rounded off, the primary apical cell is difficult to distinguish and the fronds possess a marginal meristem with numerous apicals ((475) p. 236, (744) p. 71).

The edge of the thallus remains one-layered (fig. 171 B), but elsewhere the inner cells, formed from the segments of the apicals, cut off on either surface a single layer of cortical cells (fig. 171 A–C, *co*) which undergo further anticlinal division and thus effect a gradual widening of the frond. The central cells (*m*), on the other hand, exhibit little division and become gradually stretched and pulled apart as the cortex widens ((339) p. 253, (380) p. 31). In later stages (fig. 171 D) they appear as a branching and anastomosing system of relatively narrow, widely separated threads (*m*) with multinucleate cells. The anastomoses are due to hyphae (*hy*), which mainly originate from the central cells themselves and form secondary pit-connections at the points of junction with other members of the system. The structure of *Rhodophyllis*, though presenting some points of similarity with *Cystoclonium*, is modified in relation to the bilateral habit. The abundant branching is effected by outgrowth of one or other of the marginal apicals.

The germinating spores give rise to a small basal disc (fig. 171 I, J) which soon becomes arched (fig. 171 H). According to Killian ((339) p. 249) the two-sided apical cell (*a*) of the future thallus appears at the summit of the arch (cf. *Gracilaria*), although Nienburg ((484) p. 303) concluded that the mature fronds arose from the base of this primary upgrowth, which he regarded as representing a juvenile stage.

An analogous structure is met with in *Dilsea* (Dumontiaceae, Cryptonemiales), with a number of species in northern seas. *D. edulis* Stackh.,[1] a frequent perennial near low-water mark, has a number of thick stalked obovate fronds arising from a firm basal crust. The fronds at first possess a single apical cell, although later there is a marginal meristem (341). In the younger parts (cf. also (742) p. 71, (744) p. 83) a relatively compact medulla of elongate cells is enveloped by a cortex of rounded cells, but the abundant anticlinal division in the surface-layer leads, as in *Rhodophyllis*, to separation of the medullary threads which ultimately form a network.

Calliblepharis, belonging to the same family as *Rhodophyllis*, has a structure more like that of *Cystoclonium*. The thick fronds of *C. ciliata* (*Rhodymenia ciliata* Grev. ((276) pl. 127), a winter annual found at and below low-water mark, are either simple or forked once or twice; the margin is characteristically beset with flat pinnae (fig. 170 A). In *C. lanceolata* Batt.[2] ((387) p. 72), a summer form with narrower thalli, there is a three-sided apical cell (fig. 171 F, *a*), the segments of which bear the laterals forming the cortex (*co*) at the apical end. The inner cells of the

[1] *Iridaea edulis* Bory ((276) pl. 97); *Sarcophyllis edulis* (Stackh.) Ag.
[2] *Calliblepharis jubata* Kütz., *Rhodymenia jubata* Grev. ((276) pl. 175).

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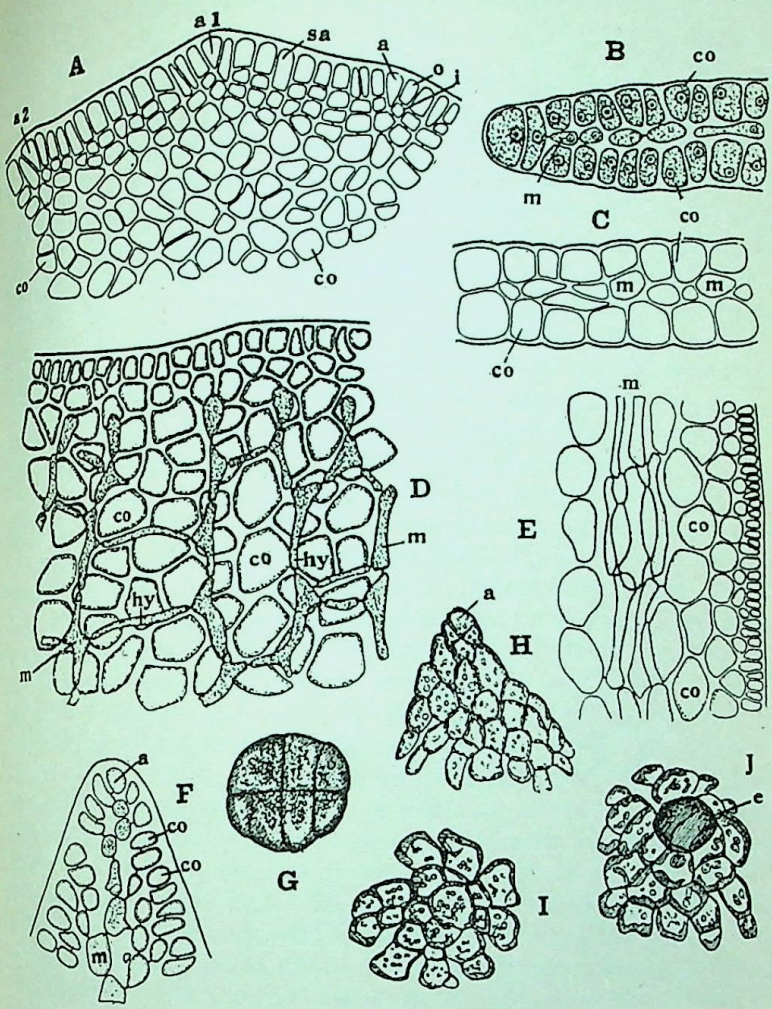

Fig. 171. A–D, G–J, *Rhodophyllis bifida* (G. & W.) Kütz.; A, apex of thallus in surface-view; B, C, transverse sections of the thallus; D, margin of thallus from above (upper cortical cells not shown); G, segmentation of spore; H–J, later stages of germling, H from the side, I and J from above. E, F, *Callithamnion blepharis lanceolata* Batt.; E, part of longitudinal section of a young branch; F, apex of thallus. *a*, apical cells; *a1*, *a2* (in A), secondary apical cells; *co*, cortical cells; *e*, commencement of erect growth; *hy*, hyphae; *i* (in A), inner segment; *m*, axial or medullary cells; *o* (in A), outer segment; *sa* (in A), segment enlarging prior to becoming a secondary apical cell. (G–J after Killian; the rest after Kylin.)

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laterals undergo great elongation and, together with the axial cells, form a central conducting tissue (fig. 171 E, *m*) linked by secondary pit-connections. The early development is like that of *Cystoclonium* ((129) p. 438).

A more specialised foliose type is afforded by *Plocamium*, of which *P. coccineum* ((276) pl. 44) is a common sublittoral Atlantic[1] seaweed. The delicate thallus, which is often only slightly flattened, is richly branched in one plane in a sympodial manner ((475) p. 228; fig. 172 A). The successive sections of the sympodium (*1–5*) bear adaxially and on their flanks a number (generally 3 or 4) of curved branches, the uppermost of which is most strongly developed; the axis is finally deflected to one side, appearing as an unbranched lateral (*l*), while growth is continued by the adjacent branch (*br 1*, *br 2*, *br 3*) which in its turn gets displaced by its uppermost lateral. The secondary branches thus occupy alternate flanks of the successive segments of the sympodium. If the tips of the branches come into contact with a firm substratum, they develop broad sucker-like haptera ((440) p. 69), a feature which has also been recorded in *Rhodophyllis bifida* ((655) p. 400).

The anatomical structure ((380) p. 49) is relatively simple. The apical cell (fig. 172 B, *a*) produces only a single series of segments (*s*) which cut off pericentrals (*p*) on either flank, the one first formed lying on the convex margin; these lateral pericentrals give rise to series of segments which, together with the axial cells, form the foundation of the median layer of the thallus. A little later the axial cells cut off two further pericentrals (fig. 172 C) which are situated in the plane of flattening. Both these and the rows of segments formed from the lateral pericentrals undergo some periclinal division. Meanwhile the central cells elongate markedly and, since they possess dense cytoplasmic contents, they form a prominent axial thread in the mature thallus (fig. 172 E, *m*). In transverse sections (fig. 172 D) the axial cell (*m*) is surrounded by 4–6 large, but relatively short, storage-cells (*co*), which are linked by secondary pit-connections; this system is continued outwards into the flanks, usually as a single layer constituted by the middle cells of the lateral rows. The surface is formed by one or two small-celled layers (*e*). The branches of the thallus arise from the lateral pericentrals (fig. 172 B, *br*).

The germinating spores ((129) p. 439, (339) p. 257, (699) p. 151) divide by two oblique walls (fig. 172 F) to form a three-sided apical cell,[2] the segments of which give rise to the small attachment-disc (fig. 172 H–J). The erect thallus (fig. 172 K, *t*) soon becomes prominent.

[1] *P. coccineum* Harv. ((272) p. 153) = *P. pacificum* Kylin ((383) p. 42).

[2] Naegeli ((475) p. 228) records a two-sided apical cell in some of the smaller branches of the mature thallus.

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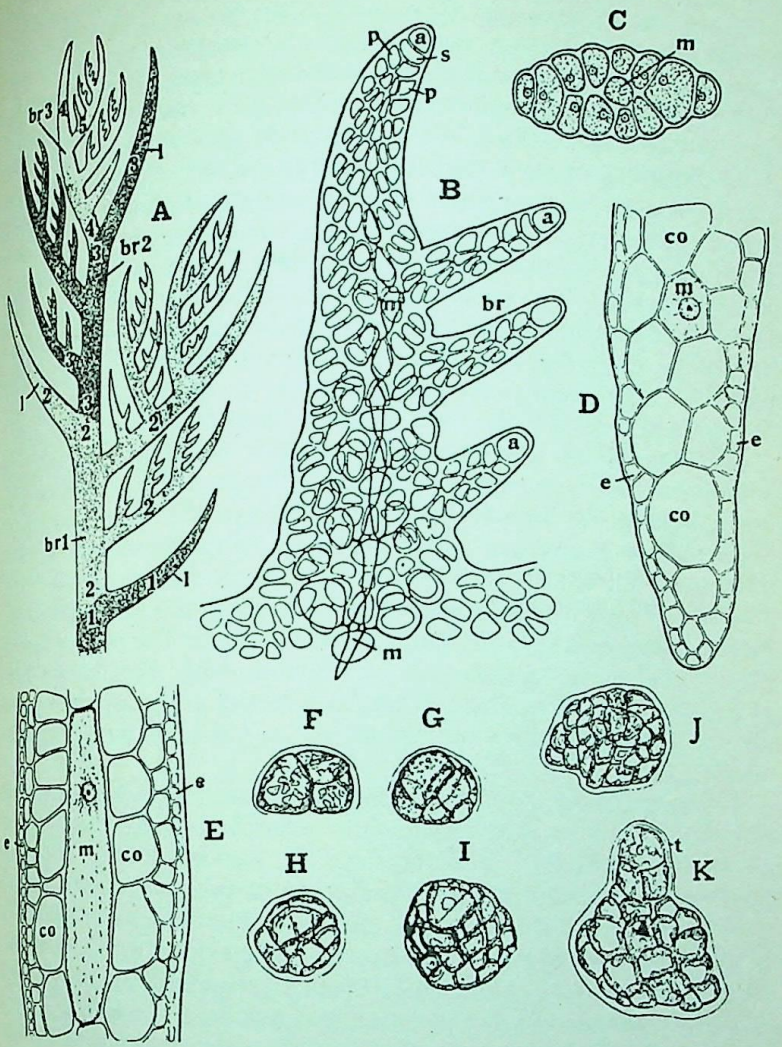

Fig. 172. *Plocamium coccineum* (Huds.) Lyngb. A, diagrammatic representation of sympodial growth and mode of branching, 1–5 being successive branch-systems, the apex of which (*l*) is deflected to alternate sides, whilst successive branches (*br 1*, *br 2*, *br 3*) carry on the growth; B, apex of a lateral branch in surface-view; C, D, transverse sections of the thallus at progressively lower levels; E, longitudinal section of thallus; F–I, segmentation of the spore; J, K, older germlings. *a*, apical cell; *br*, branch; *co*, storage-cells; *e*, superficial layer of thallus; *m*, axial cells; *p*, pericentrals; *s*, segment of apical cell; *t* (in K), commencement of mature thallus. (A after Naegeli; F–K after Killian; the rest after Kylin.)

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(*b*) *Multiaxial Forms*

The mature structure of *Agardhiella* ((587) p. 441), the species of which are characteristic seaweeds of the warmer parts of North America, resembles that of *Cystoclonium*. A number of the elongate, fleshy thalli, with numerous tapering branches, usually arise from a common discoid holdfast. The apices in *A. tenera*[1] ((50) p. 361, (387) p. 67, (505) p. 406) are occupied by 5–7 apical cells,[2] the segments of which produce on their outer side the laterals which are aggregated to form the cortex. The inner cells of the laterals give rise to down-growing hyphae, which enter into secondary pit-connections with the cells of the axial threads. In the mature thallus the medulla (fig. 173 C, *m*), consisting of a mass of narrow threads (fig. 173 B), is surrounded by a firm cortex (*co*) bounded by a narrow zone of photosynthetic cells (*e*). Near the tips the usual hairs are to be found. The spores ((173) p. 247) divide to form an irregular mass of cells.

Ahnfeltia plicata (*Gymnogongrus plicatus* Kütz. (276) pl. 288), a widespread, slow-growing perennial lithophyte (cf. (125)), readily recognised by the horny or even wiry texture of the dark purple or black thallus, is attached by a broad disc composed of vertical rows of almost cubical cells with firm walls ((363) p. 198; cf. *Polyides* and *Platoma*). Though often occurring in rock-pools near low-water mark, more robust specimens are found in deeper water. The mature thallus (fig. 173 A) shows irregular, in part dichotomous, ramification ((351) p. 348), with promiscuous adventitious branches on the older parts. One or two dichotomies are stated ((331) p. 32) to be formed in each season.

The apex ((558) p. 557) is occupied by numerous closely aggregated threads. In the mature thallus the extensive medulla consists of elongate thick-walled cells (fig. 173 D, *m*), no doubt fulfilling a mechanical function ((742) pp. 13, 29) and merging into a cortex composed of small, radially arranged, elements. The older parts, especially in plants exposed to rough seas ((256) p. 541), exhibit extensive secondary thickening ((331) p. 8) which takes place periodically by division of the peripheral cells of the cortex and results in the formation of a number of successive strata (fig. 173 D, *co*), consisting of cubical, radially arranged cells. The rather ill-defined limiting layers, marking periods of cessation of thickening, are composed of somewhat smaller elements with more deeply pigmented contents and thickened radial and inner walls. The secondary tissues of adjacent branches sometimes fuse and become enveloped by further strata common to both.

[1] *Rhabdonia tenera* J. Ag.; *Solieria chordalis* Harv. ((272) p. 121). Kylin ((383) p. 36) regards the Pacific form as a distinct species—*A. Coulteri* (Harv.) Setch. (*Rhabdonia Coulteri* Harv.); cf. also *A. ramosissima* (Harv.) Kyl. (*Rhabdonia ramosissima* J. Ag. (50) p. 365).

[2] Kylin (cf. also (50) p. 362) disputes Osterhout's statement that this form is uniaxial.

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According to Jönsson ((331) p. 32) new strata develop whenever a fresh dichotomy is formed, so that one stratum would correspond to each such period of growth. The number of strata is in general directly related to the age of the thallus ((532) p. 63), but they do not always increase in number from above downwards and are commonly more numerous on one side of the frond than on the other ((558) p. 559).

The spores of *Ahnfeltia* ((77) p. 287, (125) p. 350, (129) p. 429, (558) p. 565, (564) p. 19) give rise to small violet-coloured discs bearing hyaline

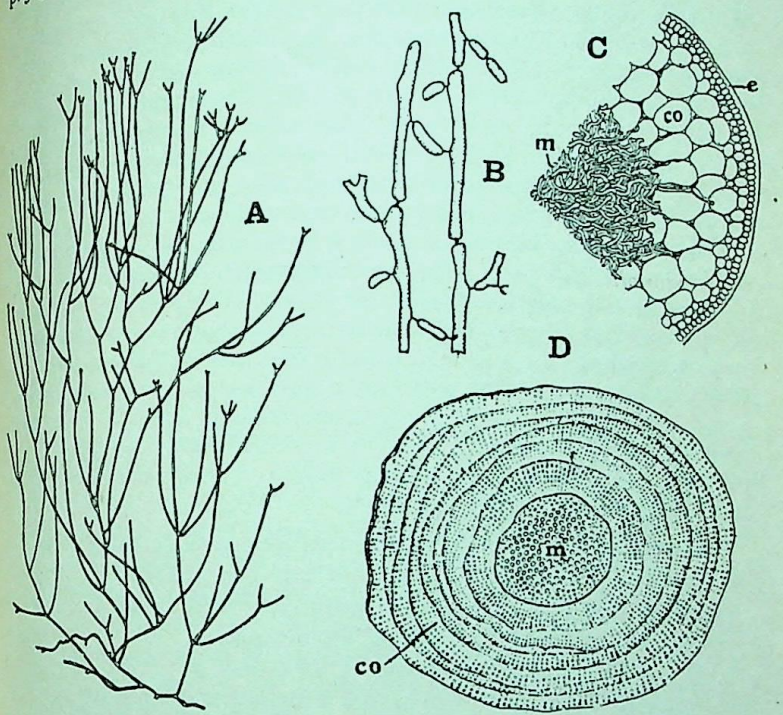

Fig. 173. A, D, *Ahnfeltia plicata* (Huds.) Fries; A, habit; D, transverse section of an older branch, showing secondary thickening. B, C, *Agardhiella tenera* (J. Ag.) Schmitz; B, medullary threads; C, part of transverse section of thallus. *co*, cortex; *e*, surface-layer of thallus; *m*, medulla. (B after Kylin; D after Jönsson; the rest after Taylor.)

hairs and forming secondary discs from the ends of marginal threads. The discs may reach a considerable size before an erect thallus is produced.

Gymnogongrus, a lithophyte closely related to *Ahnfeltia*, possesses small, repeatedly forked thalli, attached by a basal disc. In *G. Griffithsiae* (Turn.) Mart. ((276) pl. 108), widespread near low-water mark in the North Atlantic, the segments are terete, while in other species (e.g. *G. norvegicus*, fig. 174 D) they are markedly flattened. According to Jönsson ((331) p. 18) some species show secondary thickening similar to

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that of *Ahnfeltia*. The early stages have been described by Chemin ((107), (123), (128), (129) p. 424).

A foliose development of the thallus is met with in occasional representatives of diverse families of Gigartinales, e.g. *Nemastoma* (Nemastomaceae) and *Halarachnion* (Furcellariaceae). The former ((393) p. 7), with species in warmer seas (once recorded from Guernsey, (436) p. 24) and in the Southern Hemisphere, has a structure much like that of *Platoma*; in *N. canariensis* J. Ag. ((53) p. 10) large vesicular cells terminal on the subcortical filaments are recorded. *Halarachnion ligulatum* (Woodw.) Kütz. (*Halymenia ligulata* J. Ag. (276) pl. 112), a North Atlantic and Mediterranean species, resembles *Calliblepharis* in habit, though the degree of branching and flattening vary. The apex is like that of *Agardhiella* ((387) p. 61, (558) p. 163). The mature thallus (cf. also (39) p. 22,[1] (68) p. 44) shows a 2–3 layered cortex surrounding the long and widely separated threads of the medulla; hyphae are present. The germinating spores ((39) p. 6, (129) p. 358) give rise to a discoid prostrate system with an obvious filamentous construction.

Much the same internal structure is seen in the Arctic *Turnerella septentrionalis* (Kjellm.) Schmitz (*Callymenia septentrionalis* Kjellm.) (cf. (532) p. 66) and *Opuntiella californica* (Farl.) Kylin (*Callymenia californica* Farl.), both with a broad thallus, possessing characteristic peripheral glandular cells which penetrate deeply into the underlying tissues ((383) p. 23, (384) p. 282, (394)). Similar cells (fig. 252 F, *gl*; (124) p. 644, (383) p. 21) occur in *Schizymenia Dubyi* (Chauv.) J. Ag.[2] (*Callymenia Dubyi* Harv. (276) pl. 123), an ally of *Platoma* (595), likewise possessing a broad, sometimes lobed, thallus. The spores germinate like those of *Dumontia* ((129) p. 370).

A number of common foliose members of Gigartinales belong to the Phyllophoraceae and Gigartinaceae. The species of *Phyllophora* (158) are widespread northern lithophytes with small thalli, usually showing dichotomous branching in one plane. In *P. membranifolia* (fig. 174 A, C; (276) pl. 163) and *P. Brodiaei* (fig. 174 B; (276) pl. 20) the flattened fronds are borne on a cylindrical stalk (*s*), but in *P. epiphylla* Batt. (*P. rubens* Grev. (276) pl. 131) the stalk is winged throughout and not sharply demarcated; in this species the lower parts of the flat fronds show a perceptible midrib (due to secondary thickening, cf. below). *Stenogramma interrupta* Mont. ((276) pl. 157), a widely distributed form more characteristic of warmer waters, has a similar habit (fig. 170 D) and much the same structure ((387) p. 52).

The mature thallus of *Phyllophora membranifolia* (fig. 174 A) bears numerous forked fronds with the convex surface facing the source of light; in the major dichotomies one fork develops into a fan, while the other forms a continuation of the stalk ((558) p. 514). In *P. Brodiaei* and

[1] According to Rosenvinge ((558) p. 163) this possibly relates to another species.

[2] Synonymous with *Halymenia Dubyi* Chauv. and *Turnerella atlantica* Kylin ((389) p. 42; cf. (124) and (393) p. 9). *T. pacifica* Kylin ((383) p. 21, (389) p. 38) is also a species of *Schizymenia* (*S. pacifica* (393) p. 10).

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P. epiphylla older plants tend to produce numerous proliferations, mainly arising from the margins in the former and from the surfaces of the fronds in the latter. Minute, flat or nearly terete outgrowths, arising on the upper margins of the leafy fronds (fig. 174 C, *f*), produce the reproductive organs (p. 670).

The thalli last for several years and the successive increments are often recognisable. The new bright red fronds of *P. Brodiaei* ((158) p. 15, (558) p. 522) arise in spring from the apices of those of the previous season (fig. 174 B, *nf*), but in older plants most of the new growth is furnished by the adventitious shoots above mentioned. In *P. membranifolia* ((558) p. 514) the new season's growth, especially in older plants, often originates from the stalk or from the margin of the old frond, in the form of cylindrical proliferations which do not develop into complete fans until the next season.

A number of thalli usually arise from a lobed basal crust ((158) p. 23), the upper part of which is composed of dense vertical rows; the lobes sometimes grow over one another, leading to stratification of the crust. In *P. Brodiaei*, which is often found on shells of Molluscs, multiseriate haptera are formed which penetrate the latter and produce filamentous branches growing horizontally between the layers of the shells. The young discs consist of a single layer of radiating filaments ((158) p. 27); for other stages in development, see (558) p. 530, (563) p. 30. The early development of *Stenogramma* is like that of *Chondrus* ((129) p. 434).

The multiaxial structure is difficult to recognise in *Phyllophora* ((157), (158) p. 18, (742) p. 65, (744) p. 79).[1] The compact medulla consists of rather short cells with firm walls and shows a gradual transition to the cortex, each cell of which contains a large parietal chromatophore ((158) p. 30). Older parts exhibit secondary thickening owing to periclinal division of the superficial cells ((158) pp. 11, 19, (331) p. 19, (354) p. 111); such activity is, however, often localised, leading to the formation of elongate oval patches which occupy the base of the stalk and the attaching disc (fig. 174 G, *se*) or develop around the points of origin of the branches (fig. 174 F, *se*), while in *P. epiphylla* the more or less evident midrib results from such growth. These localised thickenings are no doubt of mechanical significance. As in *Ahnfeltia*, the secondary tissue shows strata representing successive periods of meristematic activity, the limiting layers being constituted by cells with thicker walls and narrower lumina.

The Gigartinaceae include the common seaweeds *Chondrus crispus* (Irish Moss, Pearl Moss, fig. 174 H; (276) pl. 63), with many different forms ((261) p. 352, (369) p. 123, (558) p. 505, (688) p. 146), and *Gigartina stellata* (fig. 174 I; *G. mamillosa* (G. & W.) J. Ag. (276) pl. 199) which are the usual sources of carrageen (p. 400). Both possess dichotomously branched thalli with a basal stalk-like portion. *Chondrus crispus* is a North Atlantic lithophyte, which is most typically de-

[1] Kononow's record ((354) p. 110) of a 3-sided apical cell in *P. nervosa* Grev. is no doubt erroneous.

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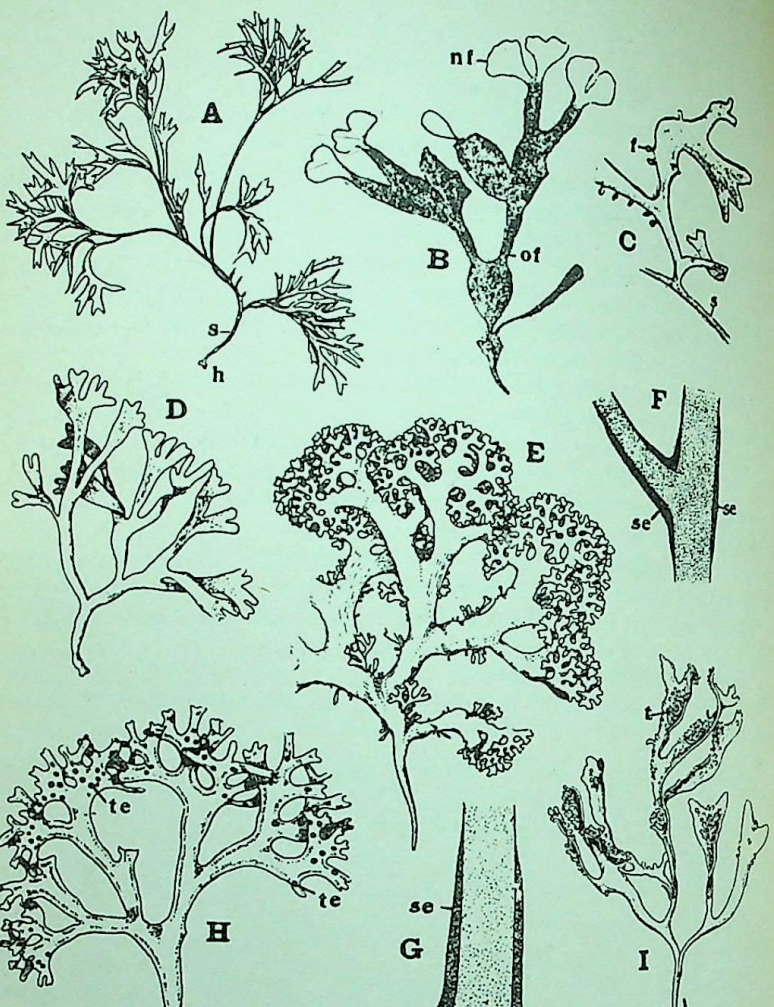

Fig. 174. A, C, *Phyllophora membranifolia* (G. & W.) J. Ag.; A, habit; C, small part of thallus showing female nemathecia (*f*). B, F, G, *P. Brodiaei* (Turn.) Ag.; B, habit showing new (*nf*) and old (*of*) fronds; F, G, diagrammatic representation showing position of secondary thickening (*se*). D, *Gymnogongrus norvegicus* (Gunn.) J. Ag. E, H, *Chondrus crispus* (L.) Stackh., different growth-forms, in H with tetrasporangia (*te*). I, *Gigartina stellata* (Stackh.) Batt., showing the teat-like outgrowths (*t*). *h*, haptera; *s*, stalk. (B after Rosenvinge; C, F, G after Darbishire; H after Fritsch and Salisbury; the rest after Taylor.)

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veloped in a limited zone near low-tide level ((161) p. 29, (333a) p. 15), the thalli occurring at higher levels often being stunted. Sublittoral forms are elongate with narrow branches. The margins of the fronds are smooth or fringed with numerous leafy processes (fig. 174 E).

The fronds of *Gigartina stellata*, usually found on rocks near low-water mark, often possess incurved edges and are not uncommonly twisted (fig. 174 I). Apart from this, fertile plants are readily distinguished from those of *Chondrus* by the numerous teat-like outgrowths (*t*) which harbour the cystocarps. This feature is distinctive of all *Gigartinas* (11, 624, 625), which for the rest show a rather variable habit. In *G. acicularis* (Wulf.) Lamour. the thalli are almost terete, whilst in some species they form a broad, almost unbranched, expanse. In still others (e.g. *G. Teedii* Lamour.) the branching is irregularly pinnate.

Both *Chondrus crispus* and *Gigartina stellata* (cf. also (324, 498)) are attached by an orbicular disc giving rise to a number of erect fronds (fig. 175 D); in *Chondrus* it may reach a width of 2 cm. ((161) pp. 15, 34, (558) p. 499). These discs (fig. 175 E) consist of vertical rows of cells with firm, non-gelatinous walls, and in *Gigartina* ((558) p. 509) they show zoning indicative of periodic growth. The spores of *Chondrus* ((129) p. 433, (161) p. 26, (379) p. 12, (558) p. 504) divide to form a hemispherical cushion which develops into the attaching disc, the production of erect thalli being deferred for some time; the early development of *Gigartina* ((129) p. 433, (699) p. 151) seems to be similar. Both the attachment discs and the erect fronds are perennial, those of *Chondrus* ordinarily lasting for two or three years ((532) p. 58, (558) p. 500). Old fronds become severed at the very base at the commencement of winter, leaving evident scars.

The thallus of *Chondrus*[1] affords clear evidence of a multiaxial construction, both in the apices ((351) p. 704) and in sections of the maturer parts (fig. 175 A, B). The medulla (fig. 175 B, *m*) consists of elongate cells with thick mucilaginous walls, their narrowed ends (*p*) being bridged by delicate septa which no doubt represent the pit-membranes; there are also secondary pit-connections (*s*) between the cells of adjacent rows. Near the surface the axial threads bear numerous perpendicular, small-celled, laterals (*oc*) which form a compact cortex, separated from the central conducting region (*m*) by cells of intermediate size (*ic*); the latter are joined by pit-connections, both to the inner and outer cells. According to Darbishire ((161) p. 19) there is a single chromatophore in each cortical cell, while the medullary cells contain a number of rounded leucoplasts. Hairs are of rare occurrence ((558) p. 502). The considerable surface-enlargement leads to a marked distortion of the older medullary elements.

[1] See (161) p. 10, (380) p. 19, (558) p. 501, (708) p. 152, (744) p. 82.

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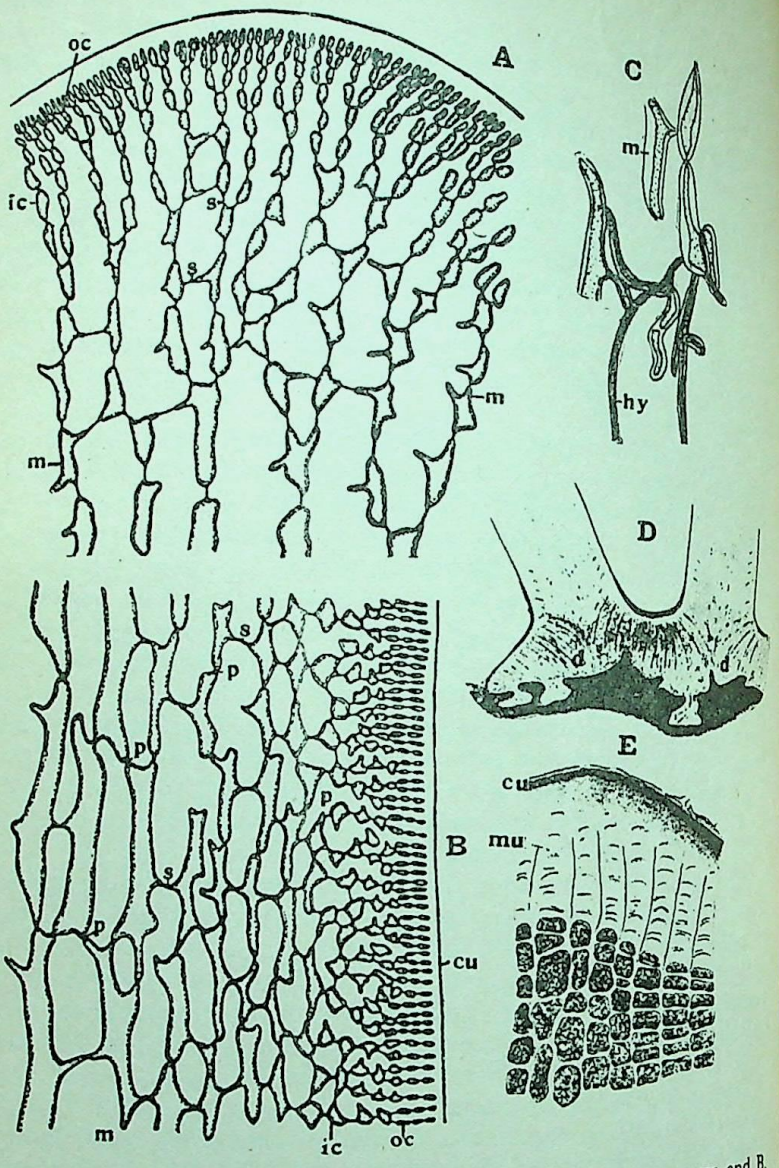

Fig. 175. A, B, D, E, *Chondrus crispus* (L.) Stackh.; A, transverse and B, longitudinal section of mature thallus; D, vertical section through attaching disc (*d*) and bases of two fror ds; E, upper part of a little of the attaching disc in vertical section. C, *Gigartina stellata* (Stackh.) Batt., small part of central tissue. *cu*, cuticle; *hy*, hyphae; *ic*, inner cortex; *m*, medullary cells; *mu*, mucilage; *oc*, outer cortex; *p*, primary and *s*, secondary pit-connections. (A, B after Kylin; C after Rosenvinge; D, E after Darbishire.)

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The structure of *Gigartina* ((558) p. 509, (634) p. 46) is essentially the same, but in *G. stellata* the cells of the inner cortex and medulla produce downgrowing septate hyphae (fig. 175 C, *hy*) which are sometimes joined to the medullary cells by secondary pit-connections. The accounts of Olson (498) and Humphrey (324) contribute little.

The widely distributed Callymeniaceae comprise forms with broad, often dichotomously branched thalli which possess a several-celled apical meristem, although, in the finer segments of *Euthora cristata* (fig. 176 A; (1) p. 11; *Rhodymenia cristata* Harv. (276) pl. 307, (745) p. 107),

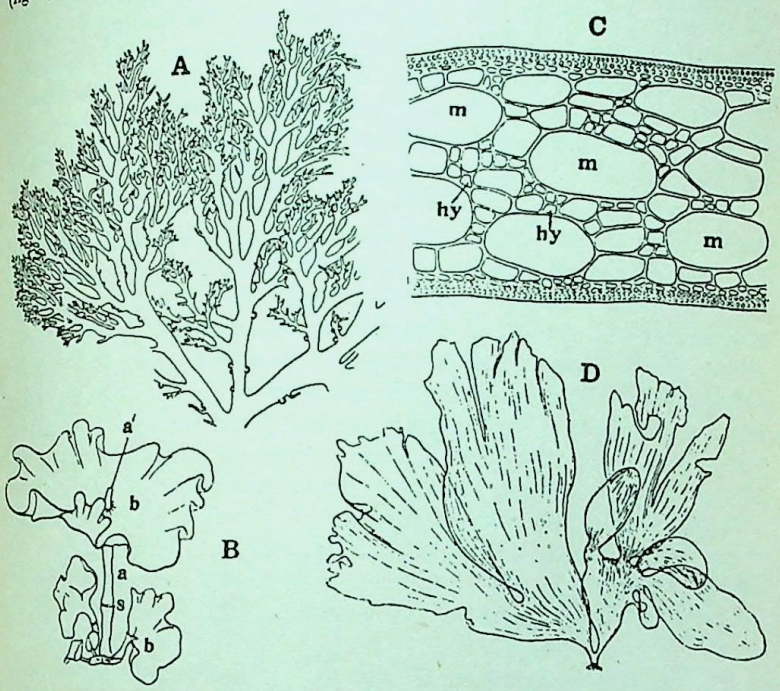

Fig. 176. A, *Euthora cristata* (L.) J. Ag., habit (after Taylor). B, *Constantinea Rosa marina* (Gmel.) Post and Rupr. (after Freeman). C, *Callophyllis edentata* Kyl., part of transverse section of thallus (after Kylin). D, *Callymenia reniformis* (Turn.) J. Ag., habit (after Newton). *a*, *a'*, stipe; *b*, frond; *hy*, hyphae; *m*, medullary cells; *s*, scar left by frond.

Kylin ((389) p. 29) found a single two-sided apical cell. Both here and in *Callophyllis* ((634) p. 56) there is a large-celled medulla (fig. 176 C, *m*) with interspersed hyphae (*hy*), but in *Callymenia reniformis* ((276) pl. 13) the medullary elements are narrow ((387) p. 59, (777)). The latter (fig. 176 D) is a typical Atlantic seaweed, while *Euthora cristata* is a deep-water subarctic form ((45) p. 36, (332) p. 136, (333) p. 13, (558) p. 596). It is not certain that these two genera are really multiaxial. The Australian *Callymenia cribrosa* Harv. ((277) pl. 73) develops numerous holes in the thallus, as in some Laminariales. The early development of *Callymenia* is much like that of *Phyllophora* ((129) p. 426, (339) p. 273), while the

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spores of *Callophyllis* divide to form a compact disc ((129) p. 436, (701) p. 74).

Two members of Cryptonemiales—*Constantinea* ((222), (529) p. 17, (537) p. 178, (599) p. 520, (614), (623) p. 355), confined to the North Pacific and the Behring Sea, and the Antarctic *Nereoginkgo* ((405) p. 15)—show a sympodial construction. Each segment of the sympodium consists of a simple or branched stalk (fig. 176 B; 177 G, *a*) terminating in a horizontal foliar expanse (*b*), growth being continued by the development from the latter of a new cylindrical segment (*a'*) which in its turn expands in the same way. The fronds, which in *Constantinea* often appear perfoliate, later split into segments and ultimately wear away leaving scars (*s*) on the stipe. A similar habit is seen in the Mediterranean *Neurocaulon reniforme* (Post. & Rupr.) Zanard. (763) p. 160; *Constantinea reniformis* Post. & Rupr. ((286) p. 146), a member of Gigartinales, but here the fronds are reniform.

The preceding consideration of certain more specialised Cryptonemiales and Gigartinales again serves to emphasise the fundamental correspondence between the uni- and multiaxial types—in fact several (*Cystoclonium*, *Catenella*) of the uniaxial forms are in the mature condition to all intents and purposes multiaxial. The foliose habit, which can be based on either type of construction, probably represents the most specialised condition reached in Gigartinales. While diverse members of Cryptonemiales and Gigartinales afford distinct evidence of heterotrichy in the early stages of development (fig. 171 H, I), the germinating spores in many genera produce a compact, often hemispherical, cushion (figs. 167 I, J; 172 J, K) from which the erect frond arises; a similar cushion is met with commonly in Rhodymeniales (p. 515). It appears to represent a modification of the filamentous prostrate system prevalent among Nemalionales.

9. Crust-forming Types among Cryptonemiales

In certain Cryptonemiales (Cruoriaceae, Squamariaceae) the mature thalli are encrusting, forming thin, circular or lobed, reddish- or dark-coloured sheets (figs. 177 A; 178 F), which are probably for the most part perennial; they are commonly found on rocks and shells between tide-marks and in deeper water, although some are epiphytic. The crusts, which adhere along the whole of their lower surface to the substratum, consist of a basal layer of closely aggregated radiating filaments (fig. 177 E) produced from the germinating spore ((339) p. 240). All the cells bear erect threads (fig. 177 B, *e*), which are simple or little branched (fig. 177 C, D), are held together by tough mucilage and form the main substance of the crust (cf. *Ralfsia*, *Lithoderma*); they either bend up gradually (*Petrocelis*, *Cruoria*) or stand off at right angles to the basal layer (*Peyssonnelia*, fig. 177 B). Attachment is usually effected by short rhizoids (*r*), the tips of which

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fit into all the irregularities of the substratum ((50) p. 129, (558) p. 174, (727) p. 256). The various genera are for the most part distinguished by reproductive features.

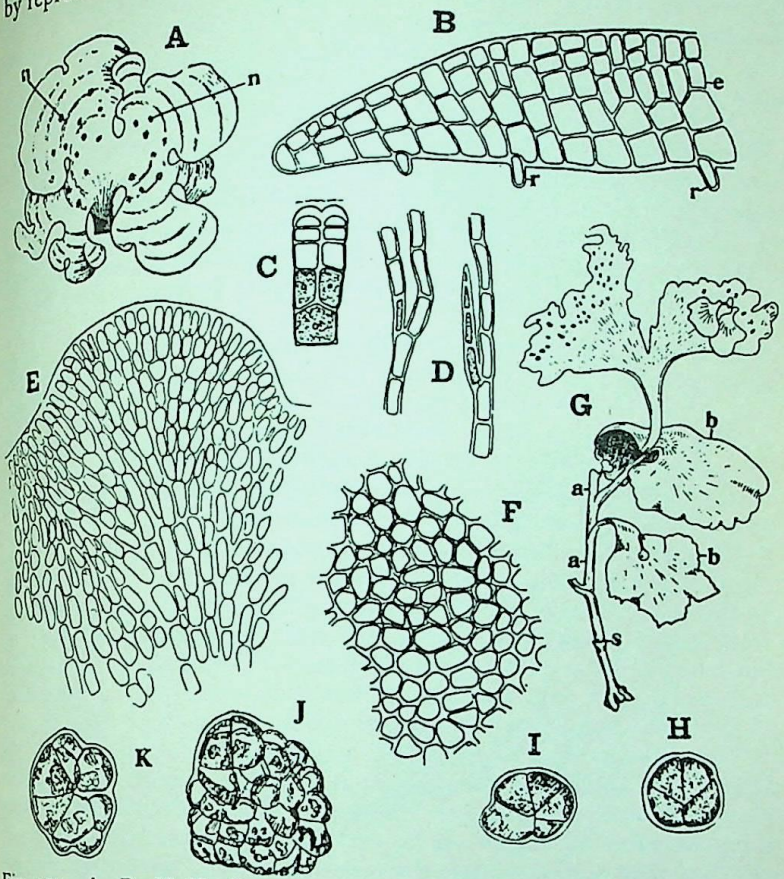

Fig. 177. A, B, H–K, *Peyssonnelia*; B, *P. Dubyi* Crouan, the others *P. squamaria* (Gmel.) Decsne; A, habit; B, section of crust; H–K, early stages in development. C, F, *Hildenbrandia rivularis* (Liebm.) J. Ag.; C, upper part of erect thread; F, surface-view of stratum from above. D, *Cruoria pellita* (Lyngb.) Fries, two erect threads. E, *Petrocelis Hennedyi* (Harv.) Batt., basal stratum from below. G, *Nereoginkgo adiantifolia* Kylin, habit. *a* (in G), stalk; *b*, frond; *e*, erect thread; *n*, nemathecium; *r*, rhizoid; *s* (in G), scar. (A after Kützing; C, F after Fritsch; E after Rosenvinge; H–K after Killian; the rest after Kylin.)

Of frequent occurrence is *Peyssonnelia Dubyi* Crouan[1] ((276) pl. 71, (577) p. 148), with small concentrically zoned crusts (cf. fig. 177 A)

[1] *Cruoriella Dubyi* (Crouan) Schmitz of various authorities. The genus *Cruoriella* ((148) p. 289, (727) p. 281) is often regarded as a subgenus of *Peyssonnelia* (cf. (50) p. 129), distinguished by the characters of the basal stratum. *Polystrata* (301) should also be referred to *Peyssonnelia* (cf. (666) p. 255).

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which commonly overgrow one another. Both here and in other species (e.g. *P. rubra* J. Ag.) the basal layer is calcified ((558) p. 193), while in some, for example *P. polymorpha* (Zanard.) Schmitz, usually found in warmer seas ((50) p. 130, (53) p. 14, (202) p. 295, (423), (762) p. 127), the brick-red crusts are impregnated with lime throughout. *P. squamaria* (fig. 177 A) is a frequent Mediterranean species forming leathery growths on *Cystoseira* ((475) p. 248, (609) p. 104).

Essentially the same structure without calcification is met with in *Rhododermis* (fig. 178 F; (2) p. 504, (26) p. 311, (149) p. 148, (357) p. 257, (360), (424) p. 42, (558) p. 197), found mainly in northern seas. In *R. Georgii* (*R. Vanheurckii* Heydr. (300); *Rhodophysema Georgii* Batt. (33) p. 377, (369) p. 194) the inner cells of the erect threads of certain forms show great enlargement (fig. 178 G, *e*), the thalli then appearing globose or irregularly lobed; such forms are connected by transitions with the usual encrusting type.

In *Petrocelis* and *Cruoria*, which are likewise uncalcified, the erect threads are less firmly connected. The fleshy growths of *P. Hennedyi* ((26) p. 314) are often found on stipes of *Laminaria Cloustoni*, while *P. cruenta* Ag. (*Cruoria pellita* Harv. non Lyngb. (276) pl. 117) is a littoral lithophyte. In the large *Cruoria pellita* ((387) p. 30, (558) p. 181) the rhizoids commonly lengthen into septate threads which may form a several-layered stratum below the older crusts.

Hildenbrandia, a genus of uncertain position allied to Corallinaceae, shows a similar habit. Most species are marine, but *H. rivularis* ((224) p. 167, (594) p. 232) is widespread (cf. (81), (434) p. 272) as a lithophyte in fresh water, being often associated with *Heribaudiella* (p. 67). Its blood-red to brown-red crusts are found in streams and lakes ((224), (239), (244) p. 507, (433), (434), (639) p. 660, (653), (767)); it is a pronounced shade-form. Only vegetative reproduction is known.[1]

The common marine species, *H. prototypus* Nardo ((558) p. 203), is a littoral and sublittoral lithophyte, in the older crusts of which the growths of successive years are marked by distinct limiting lines (sometimes also seen in *Peyssonnelia* (727) p. 259). The outer layers commonly perish in part during winter, the renewed growth being then localised at certain points and resulting in an uneven surface. Reproduction is by tetraspores which are formed in conceptacles (p. 655). The germinating spores ((129) p. 366) give rise to a short filament producing a disc at its tip.

Several genera with prostrate encrusting thalli are distinguished by the fact that laterals arise from both sides of the central axial system

[1] The accounts of sexual reproduction (70, 80, 749) are due to confusion with the colonial Myxophyceae commonly associated with *Hildenbrandia* (cf. (224) p. 186, (594) p. 232, (639) p. 667). Skuja's ((646) p. 628) record of monospores requires further investigation. Budde's ((80) p. 285) assertion that the prostrate system can give rise to chantransioid threads receives more plausible support from Starmach ((653) p. 370), although doubts remain as to the evidence for genetic connection between the two (cf. also (646) p. 626). The filamentous stages in question are identified as *C. pygmaea* and *C. chalybea*, which are known to represent the juvenile stages of *Batrachospermum moniliforme*. I have not encountered such stages during my own investigations.

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(fig. 178 B, C, *ax*); such are *Rhizophyllis*, *Coriophyllum* ((233) p. 396), and *Ethelia* ((202) p. 301, (727) p. 297). There is reason to believe that they are forms in which the prostrate habit is secondary ((400) p. 80). *Rhizophyllis Squamariae*, a Mediterranean epiphyte usually found on

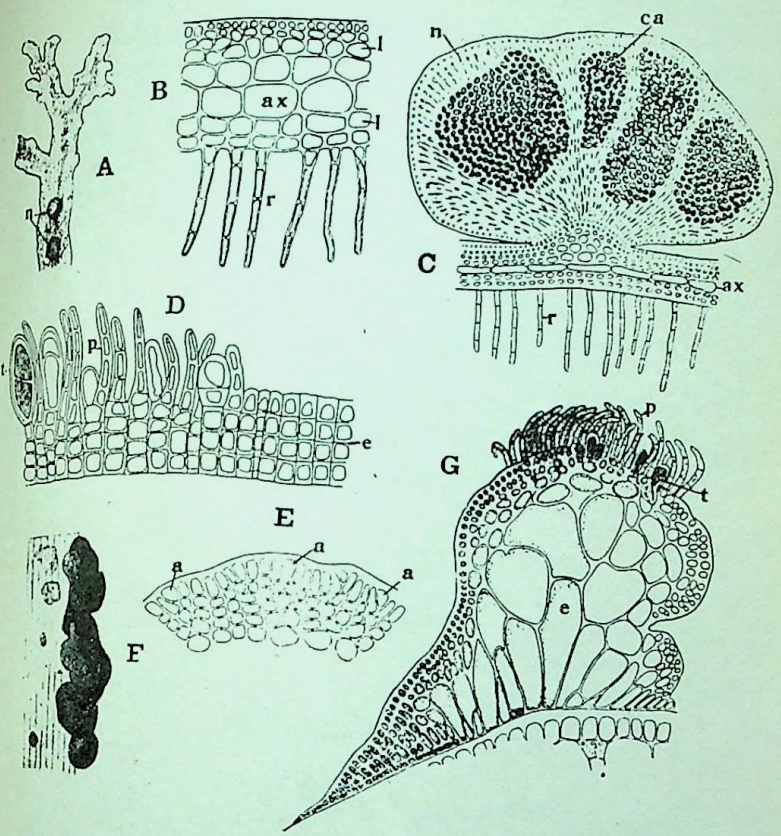

Fig. 178. A–C, E, *Rhizophyllis Squamariae* Kütz.; A, habit, with nemathecia (*n*); B, transverse section of thallus; C, longitudinal section, with nemathecium and carposporangia (*ca*); E, margin of prostrate thallus. D, F, G, *Rhododermis Georgii* (Batt.) Collins; D, vertical section of thallus, with tetrasporangia (*t*); F, habit; G, vertical section of the inflated form. *a*, apical cell; *ax*, axial thread; *ca*, carposporangia; *e*, erect threads; *l*, laterals; *n*, nemathecium; *p*, paraphyses; *r*, rhizoids; *t*, tetrasporangia. (A after Zanardini; D, G after Rosenvinge; F after Heydrich; the rest after Kylin.)

Peyssonnelia, belongs to the same family as *Polyides* ((389) p. 26; cf. also (202) p. 286). The band-shaped thallus (fig. 178 A), which is attached by septate rhizoids (fig. 178 B, *r*), possesses a series of apical cells, much as in *Rhodophyllis* (p. 490; fig. 178 E, *a*). Both here and in *Coriophyllum* the cross-section (fig. 178 B) is distinctly dorsiventral.

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Strongly calcified crusts are also typical of the Melobesieae among Corallinaceae. A relatively simple example is furnished by *Melobesia* ((526) p. 249, (545) p. 17, (558) p. 236, (652) p. 23, (659) p. 7), the thin, pink

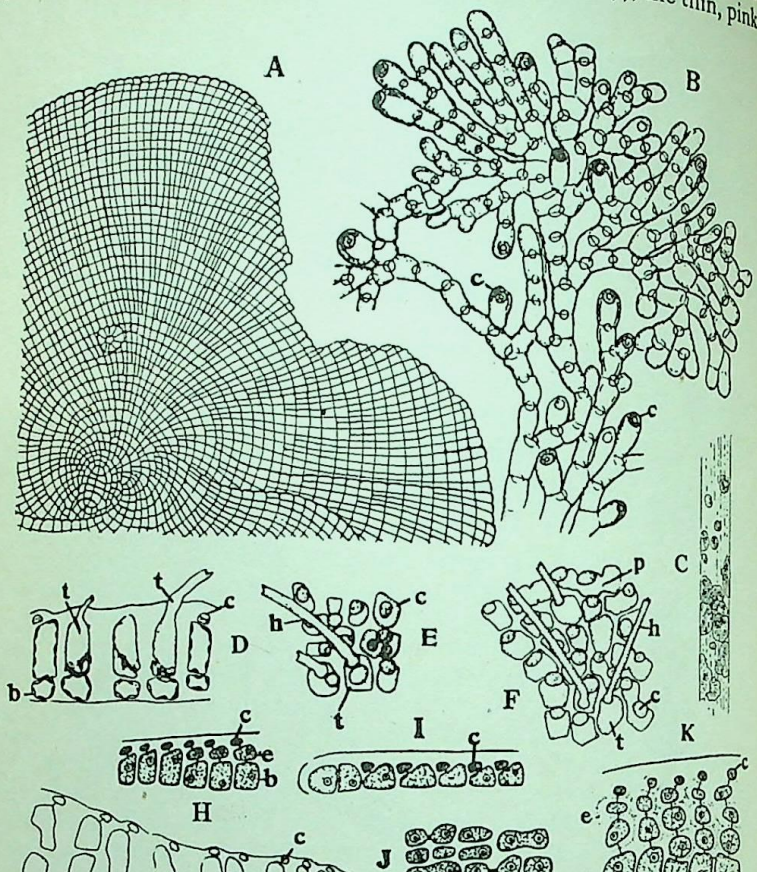

Fig. 179. A, C–G, *Melobesia Lejolisii* Rosanoff; A, surface-view of part of crust; C, habit (on *Zostera*); D, G, vertical sections; E, F, surface-view of a little of the crust. B, *M. Solmsiana* Falkenb., small part of thallus from the surface. H–K, *Epilithon membranaceum* (Esper.) Heydr.; H, I, K, radial vertical sections of the crust; J, cell-fusions. *b*, basal system; *c*, cover-cells; *e*, erect threads; *h*, hairs; *p*, points of cell-fusion; *t*, trichocytes. (A, C after Taylor; B after Solms-Laubach; D–G after Suneson; the rest after Kylin.)

or red, crusts (fig. 179 C) of which are widely distributed on all kinds of substrata (other Algae, *Zostera*, etc.), especially in warmer seas. The plants are often only a few millimetres in diameter. In many species (*Fosliella*, (320) p. 587) they consist (except in the region of the conceptacles, p. 644) of a single layer of prostrate threads (fig. 179 A),

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which show pseudo-dichotomous branching and are usually compacted to form a disc with marginal growth; the tangential septa are commonly arranged concentrically. Examples are afforded by the ubiquitous *M. farinosa* Lamour. and *M. Lejolisii* (fig. 179 A, C). In *M. Solmsiana*[1] (fig. 179 B; (192) p. 109), on the other hand, the threads of the basal stratum are commonly quite distinct, while in a similar form described by Taylor ((686) p. 10) they produce a network. In other species (e.g. *M. limitata* (Foslie) Rosenv., cf. (219)) short erect threads arise from the basal stratum so that the crusts become 2–5-layered (cf. fig. 179 G). The surface of the crusts is covered with a thick layer of mucilage. The cells of adjacent threads, both in the basal stratum and in the erect system, commonly communicate by open pores (fig. 179 F, *p*) formed by partial solution of the separating walls (cf. also (526) p. 253, (551) p. 17, (585) p. 122, (586) p. 220).

A marked feature of *Melobesia* are the flat cover-cells (fig. 179 D-G, *c*), which occur also in other Corallinaceae (p. 474). One such cell is found at the top of each erect thread (fig. 179 D, G), while in the monostromatic species they often only cover part of the subjacent cell (fig. 179 E, F) and not uncommonly overlie the septa. They may or may not contain chromatophores. Where the thallus is several-layered, the cover-cells are cut off from the cells of the basal stratum before the formation of erect threads which are produced by intercalary division of the underlying cell (cf. fig. 179 H).

Many species exhibit occasional larger hair-producing cells (fig. 179 D, F, *t*) with scanty contents and usually devoid of cover-cells ((652) p. 24); these are the *trichocytes* of Rosenvinge ((558) p. 212, (659) pp. 8, 74; "heterocysts" of Rosanoff (545) p. 57). They often originate from marginal cells which become surrounded by the adjacent growth, after the short-lived hair has been shed; before this happens a septum is formed across the base of the hair.

Epilithon membranaceum ((294) p. 408; *Melobesia membranacea* Rosanoff (545) p. 66; *Lithothamnion membranaceum* Foslie (214) p. 7, (216) p. 72), a widely distributed epiphyte lacking trichocytes, is distinguished from *Melobesia* only in details of reproduction. The thallus ((387) p. 37, (558) p. 234, (659) p. 60) may be three- or more-layered (fig. 179 H, K) and shows similar cell-fusions (fig. 179 J).

Lithophyllum and *Lithothamnion* (often written *Lithothamnium*) are lithophytes which usually possess considerably thicker crusts, frequently attached to the substratum only by their older parts. The crusts (see frontispiece) commonly exhibit foliose lobes (*F*) or irregular, sometimes coralloid (especially in *Lithothamnion*), upgrowths (*C–E*) which are often densely aggregated. The young stages closely resemble *Melobesia* ((545) p. 25). While *Melobesia*, *Lithophyllum*, and *Lithothamnion* show clear differences in reproductive details, the

[1] *M. callithamnioides* Falkenb., non Crouan; *M. farinosa* Lamour. var. *callithamnioides* Foslie ((652) p. 58).

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delimitation of vegetative material presents considerable difficulties (221), and there is much difference of opinion between leading authorities as to the placing of certain species. The encrusting forms (*A*, *I*, *J*) of the last two genera, moreover, vary considerably in habit according to the substratum and the depth at which they grow ((186), (212) p. 29), as well as through the activities of boring Molluscs ((216) p. 5) and the like.

Lithophyllum incrustans Foslie ((221) pl. 58) is widespread in rock-pools on exposed shores where it forms thick adherent crusts. In the Mediterranean *L. expansum* Philippi (frontispiece, fig. *A*; (415) p. 176, (526) p. 243, (659) p. 20), on the other hand, the crusts are attached only at their centre and often possess numerous flat lobes with a sharp one-layered edge. *Lithothamnion lichenoides* (Ell. & Sol.) Foslie[1] (frontispiece, fig. *F*, *I*; (215) p. 6, (221) pl. 11) shows a comparable habit, but in most species of the genus the encrusting base develops short upright protuberances of various shapes, as in *L. glaciale* Kjellm. (frontispiece, fig. *C*; (221) pl. 23), a widespread northern species, and *L. polymorphum* Aresch. ((221) pl. 39; *Melobesia polymorpha*, (276) pl. 345); in *L. calcareum* Aresch. (frontispiece, fig. *B*, *G*, *H*; (221) pl. 16) these upgrowths are branched and coralloid.

In taxonomic descriptions a lower region, the *hypothallium* (fig. 180 D, *h*), is usually distinguished from an upper, the *perithallium* (*p*).[2] The hypothallium generally consists of the prostrate system and of the lower parts of the upgrowing threads, while the perithallium comprises the vertical rows which commonly make up the greater part of the crust. Where the erect system arises abruptly, as in *Lithophyllum expansum* (fig. 180 B) and *L. orbiculatum* Foslie (422), the hypothallium consists merely of the one-layered prostrate system (*h*); its cells cut off cover-cells (fig. 180 C, *c*) as in *Melobesia*, and then give rise to the erect threads which increase in length by intercalary division of the underlying cell ((659) pp. 20, 63). In certain species (e.g. *Lithothamnion lichenoides*, (415) p. 127, (545) p. 91, (659) p. 63) the hypothallium is several-layered, even at the margin (fig. 180 A, *h*), and forms a considerable part of the crust, the uppermost layer bending up to form a narrow perithallium (*p*), whilst the lowest layer shows a slight downward trend.

In such instances a multiaxial structure is recognisable (cf. also *L. polymorphum*, (286) p. 271, (545) p. 97; *L. Patena* (Hook. et Harv.) Heydr. in (502) fig. 488, 1), hypo- and perithallium being respectively comparable to the medulla and cortex of a *Corallina* ((526) pp. 246, 249, (659) p. 73); in many species of *Lithothamnion* and *Lithophyllum* (fig. 180 B), however, the hypothallium is asymmetrical and the development of offstanding threads confined to its upper side. The

[1] *Lithophyllum lichenoides* Philippi; *Melobesia lichenoides* ((276) pl. 346).

[2] See (221) p. 22, (412), (415) p. 13, (482), (526) p. 245, (545), (558) p. 209, (659) p. 19.

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extent of its development often varies with the substratum, sometimes even in one and the same individual ((217) p. 4, (652) p. 17). In *Lithothamnion* cover-cells (fig. 180 A, *c*) extend right over the growing apex ((724) p. 81; cf. *Amphiroa*).

The cells of the perithallium are usually smaller and have thicker walls. The upper ones contain plentiful discoid chromatophores, while

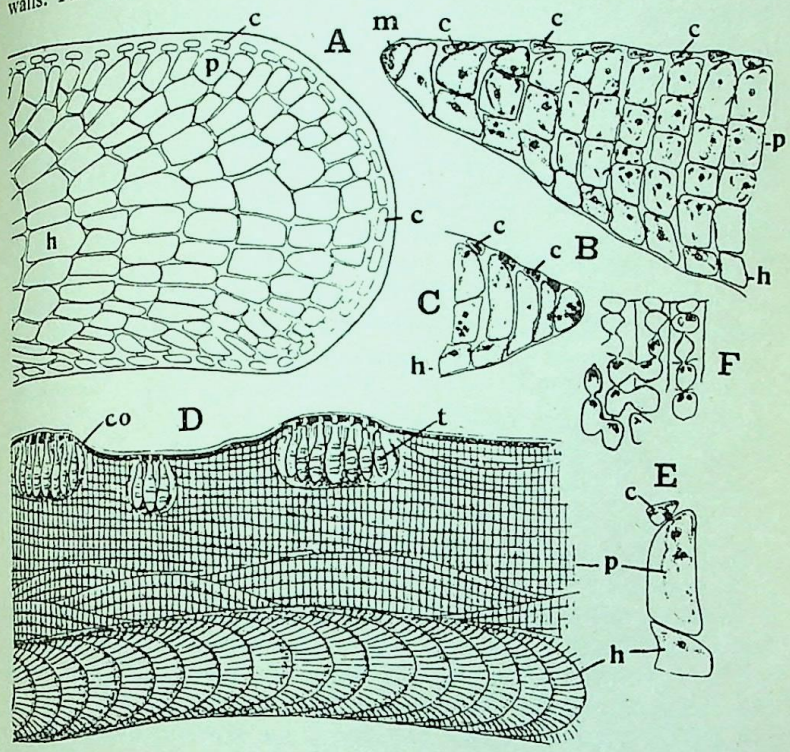

Fig. 180. A, *Lithothamnion lichenoides* (Ellis & Soland.) Foslie, section of edge of crust. B, C, E, *Lithophyllum expansum* Philippi; B, C, sections of edge of crust, showing marginal segmentation; E, single erect thread. D, *Lithothamnion Mülleri* Lenorm., vertical section of part of a crust. F, *L. norvegicum* (Aresch.) Kjellm., vertical section of part of a branch. *c*, cover-cells; *co*, sorus; *h*, hypothallium; *m*, marginal meristem; *p*, perithallium; *t*, tetrasporangium. (D after Rosanoff; F after Rosenvinge; the rest after Suneson.)

those below often include numerous starch-grains; the inner cells are often in large part dead. In *Lithophyllum* the cells of the perithallium commonly show an evident transverse arrangement and are joined by secondary pit-connections which are not produced in the customary manner ((659) pp. 22, 71). In *Lithothamnion*, on the other hand, such pits are lacking and adjacent cells fuse more or less completely (fig. 180 F) with one another (cf. *Corallina*, p. 474; *Melobesia*), a feature often

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particularly well seen in the tissue roofing the sori; when several cells are involved, branched expanses may result. *Porolithon* ((220) p. 57, (412) p. 368) differs from *Lithophyllum* chiefly in the presence of enlarged ovoid cells, occurring singly or in groups within the thallus. Trichocytes are lacking in the genera under discussion, although Rosenvinge records unicellular hairs in *Lithophyllum*. Regarding the deposition of lime, see p. 400.

The germinating spores ((129) p. 373) divide to form a compact mass of cells from which the adult thallus appears to arise as a lateral proliferation. The rate of growth of the older plants is slow ((417) p. 11). Increase in thickness of the crusts is effected by the perithallium ((415) p. 23) and localised growth results in the protuberances, commonly seen in *Lithothamnion*. Growth is periodic and the successive zones (cf. fig. 180 D), often alternately lighter and darker, are frequently (especially in *Lithothamnion*) delimited by horizontal layers of a substance which stains deeply with haematoxylin ((412) p. 326, (558) p. 212) and which is probably formed when growth ceases. Not infrequently one part of a crust grows over an adjacent one and, when this is so, each stratum may have its own hypothallium (*L. polymorphum* (558) p. 228). In *Lithothamnion* ((652) p. 26) the old tetrasporangiate sori become gradually buried and appear as small hollows in the crust.

Although the encrusting Corallinaceae attain their greatest development in warmer seas, species of *Lithothamnion* and *Lithophyllum* often form extensive sublittoral banks in temperate and polar seas ((142) p. 69, (254), (343) p. 15, (413), (414), (416), (419), (420)). A widespread species in Britain and Northern France is *Lithothamnion calcareum* (103) and in certain areas (Co. Galway, Finistère) the many fragments of the coralloid growths cast up by the waves constitute a regular *Lithothamnion* beach ((142) p. 71, (413); cf. also (333*a*) p. 16), the calcareous material of which is locally employed for liming the soil. In the Mediterranean, *Lithophyllum tortuosum* (Esp.) Foslie forms a belt at low-tide level on exposed shores ((197) p. 196, (226) p. 272, (434*a*) p. 197, (497*a*) p. 85), while other Melobesieae play an important rôle down to depths of 80 metres ((188) p. 222, (714) p. 235). There is no species common to the Arctic and Antarctic (416).

It is, however, in the oceans of the Tropics that these seaweeds, together with other calcareous Algae, Foraminifera, and Corals build up the huge calcareous masses, generally spoken of as "coral-reefs", although in several the Corals appear to play a subsidiary rôle; in all of them the encrusting Corallinaceae (Nullipores) are of prime importance as cementing organisms.[1] In the Funafuti boring they were

[1] See especially (13) p. 151, (140), (211) pp. 133, 147, (218), (229) p. 497, (230) pp. 177, 315, (231) p. 68, (315), (321), (414), (415), (620), (620*a*) p. 312, (621), (622), (662) p. 189, (723) p. 129, (724). Walther (715), however, states that the reefs between India and Ceylon are largely built up by Corals.

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found to occur abundantly down to a depth of 1000 feet. According to Foslie ((218) p. 103) the most important reef-forming species over large areas of the Indian Ocean are *Porolithon oncodes*, *P. craspedium*, *Lithophyllum Gardineri*, and *Goniolithon frutescens* Foslie; several of these are also widely distributed over many parts of the tropical Pacific (cf. also (620a) p. 318, (622) pp. 270, 276). The Melobesieae require well-aerated water for successful growth and usually occur in situations where there is a fairly strong current ((216) p. 5, (723) p. 131). At the same time a considerable number are known to thrive at very considerable depths (200–350 fathoms (622) p. 278) in clear waters in the Tropics.

The encrusting Corallinaceae occur from the Cretaceous onwards (*Archaeolithothamnion*, see p. 653) and in the Tertiary are for the most part represented by genera still living (see (525) p. 100 and (628) p. 187 and the literature there cited; also (322), (414) p. 646, (418)). They have evidently long played an important rôle, and extensive limestone rocks consisting largely of *Lithothamnion* (260) are known from various parts of the world, e.g. the Leithakalk (Miocene) of the Vienna basin ((627) p. 18) which has been used extensively as a building stone. *Solenopora* ((238) p. 442, (627) p. 20, (628) p. 189) and allied genera, grouped by Pia ((525) p. 98) in a separate family, are largely Palaeozoic (Ordovician-Jurassic) forms which are usually regarded as related to the encrusting Corallinaceae; the recent record of conceptacles in *Solenopora* (504), if substantiated, would warrant their inclusion in Corallinaceae.

The Nullipore banks are inhabited by lime-boring Algae, Molluscs, etc. ((181), (197) p. 199, (212) p. 30, (216) p. 6, (471)), which cause more or less considerable destruction of the older growth, while percolating water may convert certain parts into a structureless mass ((714) p. 242). In the deeper portions of the Funafuti boring there was a great increase in the amount of magnesium carbonate (40% or more, cf. (334) p. 373) so that the older parts of such reefs probably approximate in chemical composition to a dolomite ((134) p. 58, (307)).

10. The special Development of the Multiaxial type among Rhodymeniales

A multiaxial construction of a distinctive type is found in the genera *Champia* (704), *Chylocladia*, and *Lomentaria* which belong to the Champiaceae ((5) p. 66, (392) p. 26). The structure of the first two is similar in all essentials. *Chylocladia kaliformis*[1] ((276) pl. 145), an annual summer lithophyte, has the jointed habit (fig. 181 E) typical of many members of the family. The fistular thalli, which are attached by a minute disc, are constricted at the points at which the whorled branches arise; both here and at the bases of the branches diaphragms bridge the central cavity, which is elsewhere filled with

[1] *Lomentaria kaliformis* Gaill., *Gastroclonium kaliforme* Ardiss.

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mucilage. The entire thallus (fig. 182 C) is encased in a mucilage-envelope (*m*) with a well-marked cuticle (*cu*).

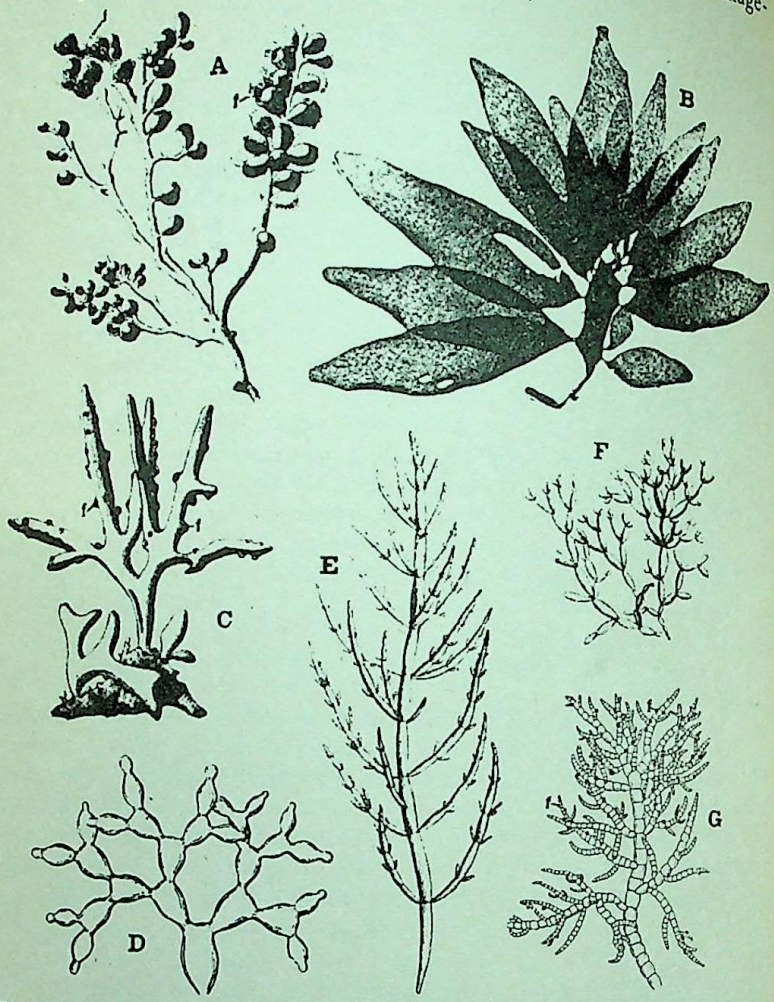

Fig. 181. Rhodymeniales. A, *Chrysimenia* (*Botryocladia*) *uvaria* (L.) J. Ag., with cystocarps (*f*). B, *Rhodymenia palmata* (L.) Grev. C, *Chrysimenia ventricosa* (Lamour.) J. Ag., older plant with cystocarps (*f*) and two young plants. D. *Coelarthrum Albertisii* (Piccone) Boerges., part of a plant. E, *Chylocladia kaliformis* (G. & W.) Hook. F, *Lomentaria articulata* (Huds.) Lyngb. G, *Champia parvula* (Ag.) Harv., part of plant bearing cystocarps (*f*). (A, C after Kuckuck; B after Rosenvinge; D after Boergesen; E, F after Kützing; G after Taylor.)

In the older parts ((284) p. 70, (289) p. 308, (380) p. 72)[1] the surface consists in the main of a single layer of radially elongated cells (fig. 182 C, *co*), with 16 to 20 little-branched threads (*l*) running longitudinally

[1] Other investigations ((168) p. 405, (744) p. 76) are not correct in all details.

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on their inner side at more or less even intervals. These longitudinal threads (fig. 182 G, *l*) converge towards the rounded apex, where they terminate in apical cells (*a*)[1] (cf. also (37) p. 686, (351) p. 704), not all situated at quite the same level (fig. 182 C). Each apical cell (*a*) cuts off a single row of segments (*s*) which divide tangentially (cf. also fig. 182 B). The outer halves constitute primary cortical cells (*co*), while

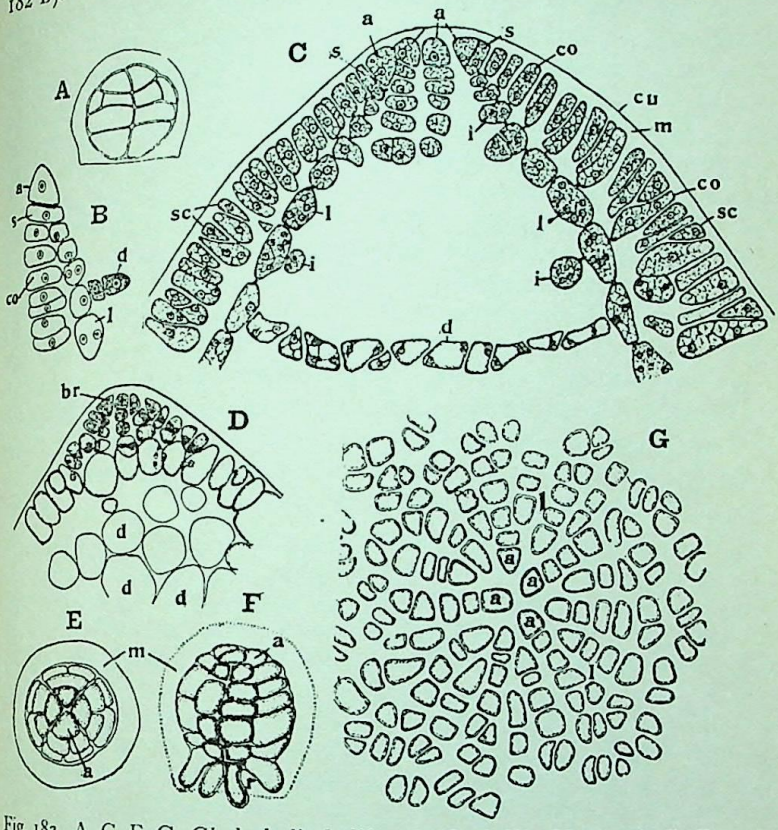

Fig. 182. A, C, E–G, *Chylocladia kaliformis* (G. & W.) Hook.; A, E, F, early stages in development, E from above, the others from the side; C, longitudinal section through apex of thallus; G, the latter from the surface. B, D, *Champia parvula* (Ag.) Harv.; B, single longitudinal thread, segmentation behind apex; D, transverse section of thallus through the point of origin of a branch (*br*). *a*, apical cells; *co*, primary cortical cells; *cu*, cuticle; *d*, diaphragms; *i*, bulb-cells; *l*, longitudinal threads; *m*, mucilage; *r*, rhizoids; *s*, segment; *sc*, secondary cortical cells. (B, D after Bliding; the rest after Kylin.)

the inner gradually lengthen to form a longitudinal thread (*l*). The primary cortical cells divide anticlinally to form the peripheral layer of large cells which contain several nuclei, numerous very small

[1] Naegeli's ((475) p. 246) and Wille's (743) statements that there is a single apical cell are erroneous (cf. also (7)).

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chromatophores, and in some localities light-reflecting bodies (p. 584). Later they cut off obliquely on their outer side a certain number of small cells (fig. 182 C, *sc*) forming a disconnected superficial layer (cf. also (558) p. 577), which is stated ((37) p. 677) to be most extensive in plants exposed to strong light. Especially in younger individuals its cells produce elongate, thick-walled hairs.

The cells of the longitudinal threads undergo no further transverse division, but most of them cut off on their inner side a small spherical cell with plentiful contents (fig. 182 C, *i*), the bulb-cells of American writers. At the points of branching of the thalli these cells divide to form threads which unite, with the establishment of secondary pit-connections, to produce the one-layered diaphragms (fig. 182 C, D, *d*). The numerous bulb-cells that do not develop into diaphragms have been interpreted as glandular elements ((289) pp. 314, 327) or, rather more usually, as undeveloped diaphragms. Similar structures occur in most Champiaceae and are also present in Rhodymeniaceae (cf. below), where diaphragms are usually lacking. Their utilisation in the formation of diaphragms is apparently a secondary feature (cf. (392) p. 35) and they are perhaps best regarded as arrested hyphae.

Branches originate by the outgrowth of several peripheral cells into threads (fig. 182 D, *br*) which unite to form the apex of the new axis ((289) p. 315, (558) p. 579); adventitious branches appear at indeterminate places in older plants.

Kylin ((392) p. 30) maintains Kützing's genus *Gastroclonium* for those species of *Chylocladia* in which the main axes and the basal parts of the branches remain solid, with only slight elongation of the inner cells (cf. (42) p. 23, (289) p. 315). The hollow parts show essentially the same structure as *Chylocladia*. *G. ovale* (Huds.) Kütz.[1] is a frequent littoral species.

Champia parvula[2] (fig. 181 G), a widely distributed epiphyte in the warmer seas of the Northern Hemisphere, forms dense bushy tufts arising from a number of creeping threads attached by multicellular haptera ((50) p. 408); the branches here often arise singly. The more robust and little-branched *C. lumbricalis* Lamour. ((270) pl. 30, (289) p. 317) has a wall of a number of layers of cells, while the diaphragms may be several-layered.

In *Lomentaria* there are no diaphragms. The thalli of *L. articulata* (*Chylocladia articulata* Harv. (276) pl. 283), which is common between tide-levels, are constricted at the points of branching (fig. 181 F)

[1] *Lomentaria ovalis* J. Ag.; *Chylocladia ovalis* (Huds.) Hook. ((276) pl. 118). In the Mediterranean *G. clavatum* (Roth) Ardiss. (*Lomentaria clavata* J. Ag.; *Chylocladia clavata* (Roth) Bliding, (42) p. 38; *C. mediterranea* J. Ag.) only the basal part is solid. *C. mediterranea* (Kütz.) Zanard. ((763) pl. 44) is *Lomentaria compressa* (Kütz.) Kylin ((392) p. 27).

[2] *Chylocladia parvula* Hook. ((276) pl. 210); *Lomentaria parvula* Kütz. For the structure of this and other species, see (37) p. 686, (41), (42) p. 5, (50) p. 407, (289) p. 321, (475) p. 247.

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where they are solid. Those of *L. clavellosa* (Turn.) Gaill.,[1] on the other hand, are hollow throughout and unconstricted; they may reach a length of 40 cm. and show distichous branching. The anatomical structure ((42) p. 41, (168) p. 411, (289) p. 323, (380) p. 44, (558) p. 583) is much like that of *Chylocladia* (fig. 183 A). The peripheral small-celled cortex (fig. 183 B, *sc*) is, however, more extensive and may form a continuous several-layered covering to the older parts. The longitudinal threads (*l*) are branched (fig. 183 C) and joined by secondary pit-connections (*p*), while in the solid nodes of *L. articulata* they are closely packed and consist of large rounded cells.

The early development[2] is similar in all Champiaceae. The spores first divide into quadrants which then segment into two horizontal tiers (fig. 182 E). The four upper cells (*a*) constitute the primary apicals which divide horizontally to produce the erect thallus (figs. 182 F; 183 E), while those of the lower tier grow out into rhizoids (*r*). As the thallus broadens, additional apical cells are formed from some of the uppermost segments. Older germlings of *Chylocladia* and *Lomentaria* show a thick, hemispherical or nearly globular attachment-organ bearing one or two erect fronds. In *L. uncinata* Menegh. ((173) p. 248) it gives rise to radiating stolons, which form secondary holdfasts at their tips.

The *Rhodymeniaceae* show greater diversity in external habit and include a number of non-fistular foliose forms (*Rhodymenia*, fig. 181 B; *Fauchea*). *Chrysimenia* (sens. lat., fig. 181 A, C), *Coelarthrum* (fig. 181 D), and *Bindera*, however, resemble the Champiaceae in possessing vesicular thalli and in the presence of bulb-cells like those of *Chylocladia* on the inner surface of the cells lining the central hollow (fig. 183 G, H, *i*). In the Australian *Bindera splachnoides* Harv. ((277) pl. 111, figs. 1, 2; *Halymenia saccata* Harv. (6) p. 41, (277) pl. 133, (392) p. 5) these terminate systems of branched threads (fig. 183 K). In all Rhodymeniaceae the inner cells are large and rounded (fig. 183 I, J; (392) p. 35), which no doubt represents a more primitive condition than that found in Champiaceae.

Rhodymenia palmata (fig. 181 B; (276) pl. 217), a widely distributed littoral perennial with a dark red, simple or branched thallus (cf. also (558) p. 569), is the dulse of the Scots and the dillisk of the Irish and is edible (see p. 411). The early stages ((129) p. 438, (340) p. 191) resemble those of Champiaceae, although the young fronds are stated to be uniaxial, the axial thread persisting in the basal stalk. The mature fronds ((94), (340) p. 198, (389) p. 35, (634) p. 30, (745) p. 99) possess a marginal meristem and consist of several layers of thick-walled medullary cells enveloped by a rather narrow small-celled cortex; in the stalk the latter is broader and in older plants shows zones of growth ((331) p. 23, (340)

[1] *Chrysimenia clavellosa* J. Ag. ((276) pl. 114); *Chylocladia clavellosa* Grev.

[2] See (129) p. 439, (162) p. 344, (173) p. 249, (339) p. 246, (379) p. 5, (558) p. 582; cf. also Solms-Laubach, *Ann. Jard. Bot. Buitenzorg*, 4, 152–3, 1884.

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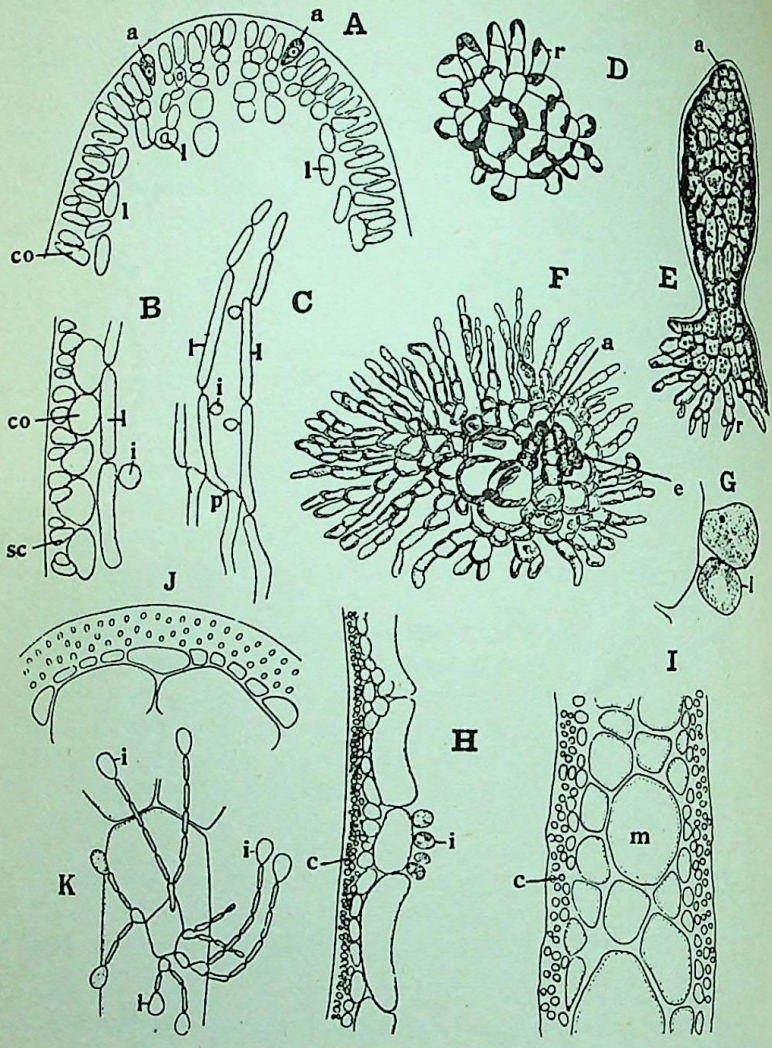

Fig. 183. A–E, *Lomentaria articulata* (Huds.) Lyngb.; A, longitudinal section of apex; B, portion of older part in longitudinal section; C, longitudinal threads showing secondary pit-connections (*p*); D, E, early stages in development, D from above, E from the side. F, *Chrysimenia* (*Botryocladia*) *microphysa* Hauck, germling, from above. G, H, *C.* (*Botryocladia*) *pseudodichotoma* Farl.; G, bulb-cells; H, longitudinal section. I, *Fauchea Fryeana* Setch., section of thallus. J, K, *Bindera splachnoides* Harv.; J, part of transverse section of thallus; K, group of bulb-cells. *a*, apical cells; *c* (in H, I), cortex; *co*, primary cortical cells; *e*, commencement of mature thallus; *i*, bulb-cells; *l*, longitudinal threads; *m*, medulla; *r*, rhizoids; *sc*, secondary cortical cells. (D–F after Killian; I after Sjöstedt; J, K after Kylin; the rest after Bliding.)

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p. 207). The attachment-disc is composed of numerous rows of cells ((701) p. 72). The young fronds bear groups of hairs which are visible to the naked eye. Butters (90) gives a few data on the structure of *R. pertusa* (Post. & Rupr.) Ag., a characteristic subarctic sublittoral species with a large thallus showing perforation ((623) p. 313). *Fauchea* ((389) p. 33, (615) p. 239, (634) p. 25), confined to warmer seas, has fronds with much the same structure (fig. 183 I) as *Rhodymenia*. *Dendrymenia* ((638) p. 16) shows a similar habit and sympodial mode of growth to *Constantinea* (p. 502).

The seaweeds usually included in *Chrysimenia* (364)[1] are frequent sublittoral forms of warmer seas, varying in the degree of inflation and the extent of branching of the thallus (fig. 181 A, C). *Coelarthrum*, widely distributed in warmer seas ((47) p. 189, (50) p. 404, (57) p. 40, (60) p. 333), as well as in Australia ((392) p. 14), has a dichotomously branched thallus (fig. 181 D), showing periodic constriction at points where diaphragms occur. The bulb cells are here borne on irregular stellate elements. The Tasmanian *Gloeosaccion* ((4) p. 316, (277) pl. 83) has a simple saccate thallus. *Halosaccion ramentaceum* (L.) J. Ag., a characteristic North Atlantic and Pacific seaweed, with a very variable habit ((361) p. 30), is often ((685) p. 304) included in the Rhodymeniaceae (cf. also (404) p. 27).

II. The special Developments of the Uniaxial type among Ceramiales

The numerous genera of Ceramiales exhibit great diversity in vegetative construction, as exemplified by the families Ceramiaceae, Delesseriaceae, Rhodomelaceae, and Dasyaceae, although these only present minor differences in their reproduction. Diverse genera attain to a high degree of morphological complexity. All Ceramiales are, however, uniaxial. Moreover the germinating spores develop a single bipolar axis from the first (figs. 184 G; 185 D, E) and all traces of heterotrichy are lacking.[2] While the first septum is usually described as running parallel to the substratum, Chemin (129) affirms that it is vertical or oblique to the latter and that the germling is at first prostrate, although the apex soon becomes erected (cf. also (483)); this is almost certainly a cultural condition. The four families are best considered separately.

[1] Kylin (392) establishes a number of distinct genera, viz. *Botryocladia*, with a partly solid thallus (incl. *C. pseudodichotoma* Farlow, (42) p. 51, (194); *C. uvaria* (L.) J. Ag. (47) p. 189, (50) p. 402, (52); *C. pyriformis* Boerges. (47) p. 187, (50) p. 400; *C. microphysa* Hauck), and *Cryptarachne* with strongly compressed thalli showing extensive hypha-formation (incl. *C. Agardhii* Harv. (272) p. 189, (50) p. 392). The genus *Chrysimenia* is retained for *C. ventricosa*. See also (778).

[2] See (129) p. 445, (173) p. 256, (339) p. 213, (380) p. 136, (558) p. 336, (692) p. 71, (695) p. 8.

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(*a*) *Ceramiaceae*

Many Ceramiaceae retain a filamentous habit, and this is very obvious in *Callithamnion*, where the structure[1] resembles that of *Acrochaetium* (p. 450). The richly branched tufts of the former (fig. 184 A), commonly only 2–5 cm. high, have much the habit of a *Cladophora* (fig. 184 B). The elongate cells are uninucleate (*C. Brodiaei* Harv. (276) pl. 129; *C. roseum* (Roth) Harv. (276) pl. 230), or more usually multinucleate (*C. corymbosum*), and mostly contain ribbon-shaped chromatophores. The branches arise alternately and in definite spiral succession (560) from just beneath the septa, usually standing off in all directions, though distichous in some species (e.g. *C. tripinnatum* Ag., *C. Hookeri*, fig. 184 B; (276) pl. 279). In many the principal axes are composed of broad, thick-walled cells (fig. 184 B, *a*) which sometimes show a zigzag disposition ((697) p. 538). Vigorous development of the laterals occasionally results in pseudo-dichotomy in the later branchings (*C. corymbosum* Lyngb. (276) pl. 272). Certain species (*C. Brodiaei*; (558) p. 314, (559)) at times produce a profusion of long slender hairs on the ultimate branches, which may continue to grow sympodially, as in *Acrochaetium*.

The older parts are usually enveloped in an investment of delicate multicellular corticating threads (lacking in *C. byssoides* Arn. (276) pl. 262) which originate from the basal cells of the laterals (fig. 184 C) and sometimes (*C. Hookeri*) also from the lower ends of the axial cells; they commonly grow through the thick walls of the latter, although ultimately penetrating to the exterior. This cortical envelope often forms a compact tissue (six cells thick in *C. tetricum* Ag. (736) p. 194; cf. also (734)) which completely obscures the lower part of the axis and may contain chromatophores in its outer cells. Not uncommonly short adventitious branches arise from it.

Anchorage is effected by similar multicellular filaments emerging from the cortex and from the basal cells of the lower branches and sometimes (*C. tetricum*) uniting to form a definite disc. The germlings are attached by a basal rhizoid (fig. 184 F, G), which is soon replaced by others. In *C. Furcellarieae* J. Ag. ((558) p. 339) attachment is aided by horizontal stolons which arise from the lower axial cells and may give rise to further erect threads. Similar structures are recorded in the minute *C. scopulorum* Ag. ((733) p. 130), where they emerge singly from the under sides of the branches and, being detachable, aid in vegetative propagation.

Certain species persist from one season to another (cf. (558) p. 329), although others are probably annuals. Several (e.g. *C. roseum*) favour mud-covered rocks near low-water mark, while others (e.g. *C. Brodiaei*)

[1] See (369) p. 150, (478) p. 358 (as *Poecilothamnion*), (558) p. 308, (692) p. 67.

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are more usually epiphytic, with rhizoids penetrating into the substratum. One of the most robust species is *C. tetricum*.

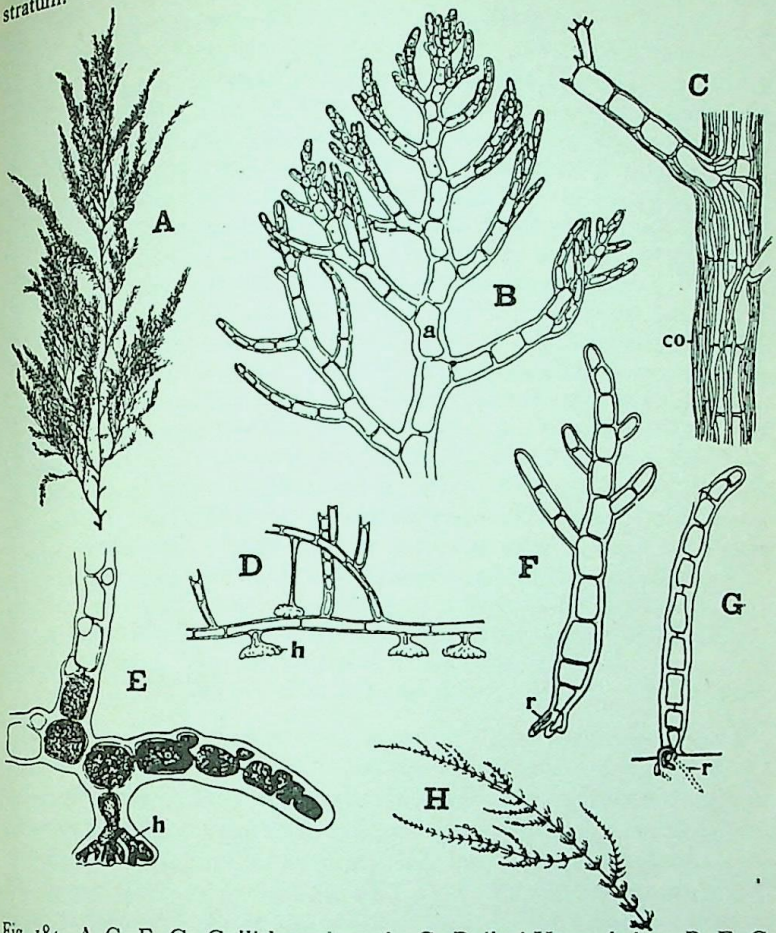

Fig. 184. A–C, F, G, *Callithamnion*. A, *C. Baileyi* Harv., habit. B, F, G, *C. Hookeri* (Dillw.) Ag.; B, apical part of a plant; F, G, young plants. C, *C. Baileyi* showing cortication (*co*). D, *Spermothamnion Turneri* (Mert.) Aresch., base of plant. E, *Trailiella intricata* (J. Ag.) Batt., base of plant. H, *Sphondylothamnion multifidum* (Huds.) Naeg., small part of a plant. *a*, axial cell; *h*, haptera; *r*, rhizoids. (A, C, D after Taylor; H after Hauck; the rest after Rosenvinge.)

Monospora, *Pleonosporium*, and *Seirospora*[1] differ from *Callithamnion* only in their reproductive features; *Seirospora Griffithsiana* Harv. ((276)

[1] This genus (*Microthamnion* J. Ag.) was established by Harvey (276) who, however, later ((272) p. 237) again included it in *Callithamnion* (*C. seirospermum* Griff., *Poecilothamnion seirospermum* Naeg.). The reproductive features (p. 728), however, warrant generic separation. Schmitz (593) believed that *Seirospora* was characterised by its uninucleate cells, but it has since been shown that these occur also in some species of *Callithamnion* (cf. above and (46) p. 13, (460) p. 288).

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pl. 21, (478) p. 364, (558) p. 347, (580)) is a rare North Atlantic sublittoral species. *Compsothamnion* ((478) p. 342, (737)), which shows distichous branching (fig. 275 H), includes a number of delicate forms found near low-tide level (cf. (276) pl. 5, 269, as *Callithamnion*), whilst *Sphondylothamnion* ((478) p. 380), with the widely distributed *S. multifidum* ((69) p. 181, (225) p. 230), is distinguished by its whorled laterals (fig. 184 H); both genera are uncorticated.

Spermothamnion ((373), (460) p. 281, (478) p. 351, (531) p. 15, (558) p. 298), *Ptilothamnion* ((69) p. 179, (387) p. 77), and *Trailiella* ((30) p. 10, (372) p. 4,[1] (373) p. 87, (432) p. 196, (558) p. 305), the last a recent introduction into Northern Europe, are uncorticated epiphytes with creeping threads attached by haptera (fig. 184 D, E); *Trailiella intricata*[2] is also distinguished by the possession of vesicular cells (p. 586) and the slight degree of branching of the erect threads. The common form of *Spermothamnion* found between tide-levels is probably correctly designated *S. repens* (Dillw.) Rosenv., while *S. Turneri* (Mert.) Aresch.[3] and other closely related forms, regarded by some as distinct species, appear to have only varietal value. The creeping filaments are persistent, while the numerous branches of the erect filaments are either opposite (usually in var. *Turneri*) or alternate (usually in var. *roseolum*); the cells are multinucleate. *Ptilothamnion pluma* (Dillw.) Thur. (*Callithamnion pluma* Ag. (276) pl. 296) is a rare, though widely distributed, form.

A similar attachment by creeping threads is seen in *Vickersia baccata* (J. Ag.) Karsak. ((54) p. 20; (336); *Callithamnion baccatum* Ag.), found in the Mediterranean ((225) p. 224) and the islands of the North Atlantic ((583) p. 55); here the opposite or whorled laterals of the erect threads are composed of single much inflated cells (fig. 289 G; p. 713).

Griffithsia ((50) p. 202, (375) p. 99, (428) p. 641, (751)) is distinguished by its huge non-corticated multinucleate cells which are readily visible to the naked eye; the older ones may contain several thousand nuclei as a result of repeated division. The copious forked branching (fig. 185 I) is due to equal development of lateral and parent axes. Short branchlets (fig. 185 J, *f*), bearing the reproductive organs, arise from the tops of the younger cells, while richly branched hairs (fig. 185 I, J, *h*) are commonly borne in the same position; both structures are deciduous. The entire thallus is encased in a thick mucilage-envelope, which in *G. corallina* is two-layered and visible to the naked eye ((258) p. 215). The early development resembles that of *Callithamnion* ((129) p. 478, (339) p. 223, (379) p. 16), the older plants being usually attached by vigorous rhizoids emanating from the basal cell of the germling ((50) p. 204, (173) p. 259, (428) p. 654).

[1] As *Spermothamnion roseolum* (Ag.) Pringsh.

[2] *Spermothamnion Turneri* f. *intricata* Holmes & Batters ((312) p. 96).

[3] *Callithamnion Turneri* (Roth) Ag. ((276) pl. 179); *Herpothamnion Turneri* (Mert.) Naeg. ((478) pp. 348, 351). Other members of this aggregate, that are sometimes distinguished as separate species, are *S. roseolum* (Ag.) Pringsh. ((531) p. 15) and *S. hermaphroditum* (Naeg.) Janczewski ((326) p. 115; *Herpothamnion hermaphroditum* Naeg. (478) p. 352).

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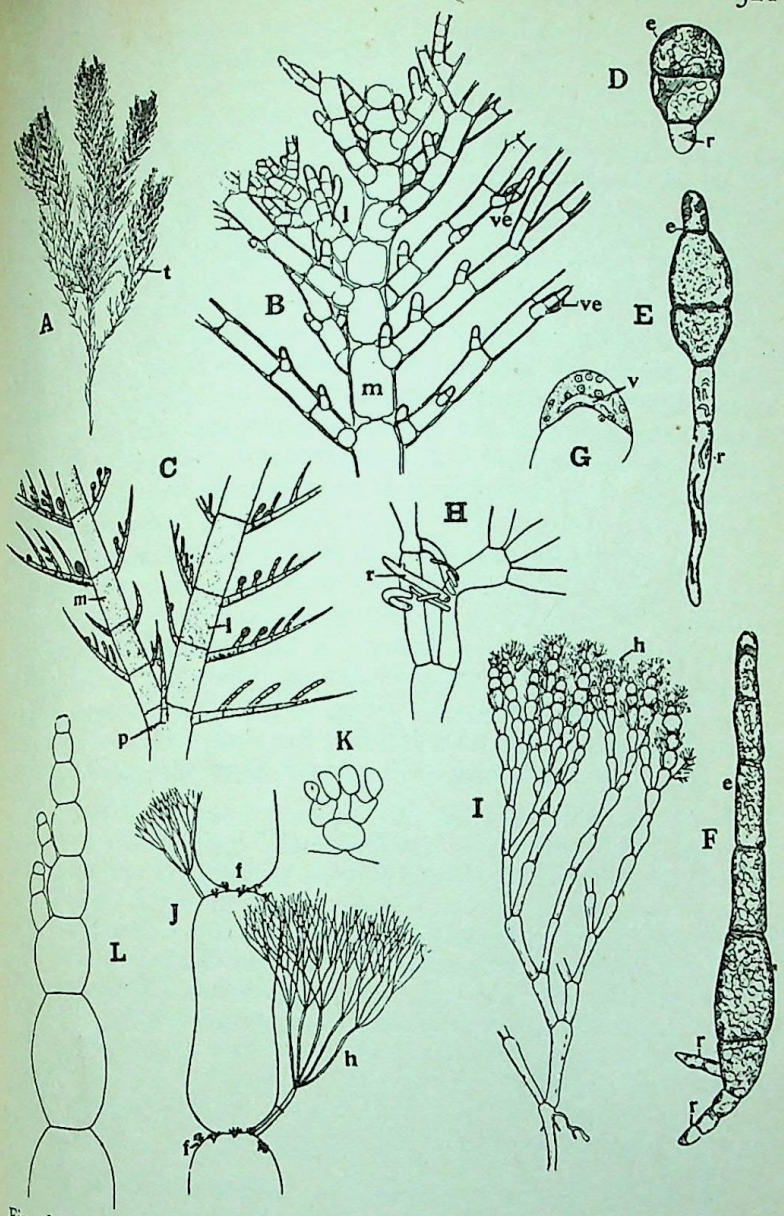

Fig. 185. A–F, *Antithamnion*; A, habit and B, part of a branch-system of *A. cruciatum* (Ag.) Naeg.; C, *A. plumula* Thur., part of branch-system; D–F, the same, successive stages in germination. G–L, *Griffithsia*; G–I, *G. globifera* (Harv.) J. Ag.; G, cell-division, formation of vacuole (*v*) in daughter-cell; H, rhizoid-formation; I, habit. J–L, *G. corallina* C. A. Ag.; J, a few segments, with fertile shoots (*f*) and hairs (*h*); K, young fertile shoots; L, apex of thallus. *e*, erect axis of young plant; *h*, hairs; *l*, branches of unlimited growth; *m*, main axis; *p*, accessory lateral; *r*, rhizoids; *t*, tetrasporangia; *ve*, vesicular cells. (A, I after Taylor; B after Rosenvinge; C after Naegeli; D–F after Killian; G, H after Lewis; J–L after Kylin.)

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The annual *G. corallina* ((276) pl. 214; *G. corallinoides* Batt.) and *G. setacea* C. Ag. ((276) pl. 184; *G. flosculosa* Batt.), stated to be perennial, are widely distributed European littoral species, while *G. globifera* (Harv.) J. Ag. (*G. Bornetiana* Farlow) is a frequent annual on the Atlantic shores of North America. *Bornetia secundiflora* (J. Ag.) Thur. (*Griffithsia secundiflora* J. Ag. (691)), with the same vegetative structure, is more characteristic of warmer seas ((436) p. 21). Another not uncommon form with multinucleate cells is *Halurus equisetifolius* Kütz. (*Griffithsia equisetifolia* Ag. (276) pl. 67), which is distinguished by its whorled branching ((478) p. 399).

Greater specialisation is evident in *Antithamnion*,[1] with several widely distributed species, usually found on rocks near low-water mark. The plants possess creeping threads which have upturned tips and bear a number of erect uncorticated filaments. Their branches are usually clearly distinguishable into those of unlimited and those of limited growth. Several branches arise from the same parent-cell and those of limited growth are either opposite, as in *A. cruciatum* (fig. 185 A, B; *Callithamnion cruciatum* C. Ag. (276) pl. 164) and *A. floccosum* (Müll.) Kleen (*C. floccosum* Ag. (276) pl. 81; *Pterothamnion* Naegeli) or in whorls of three (cf. *Crouania*, p. 459) or four, as in *A. elegans* Berthold ((36) p. 516, (54) p. 56) and *A. subulatum* (Harv.) J. Ag. ((383) p. 50); the members of a whorl develop successively. The ultimate branchlets are commonly adaxial (fig. 185 B, C). The branches of unlimited growth are alternate and take the place of a short lateral (fig. 185 B, *l*). The uninucleate cells contain numerous chromatophores.

In *A. plumula* (*Callithamnion plumula* Lyngb. (276) pl. 242) the branches of the erect threads are generally opposite and in one plane (fig. 185 C), although in shaded habitats they tend to turn in the direction of the light ((37) p. 614). Cells producing a shoot of unlimited growth (fig. 185 C, *l*) commonly lack the opposite lateral, which is also often wanting on one or two of the overlying cells of the parent branch. Frequently, however, the cell from which a long shoot arises bears a pair of unbranched laterals (*p*) in a plane perpendicular to the normal plane of branching. Occasional individuals have the branches in whorls of three or four, with the long shoots orientated in diverse directions; according to Berthold ((37) p. 614) this is a result of uniform illumination, although Rosenvinge's observations ((558) p. 364) render this doubtful.

The short laterals of *A. cruciatum* (fig. 185 B) are often decussate (cf. also (54) p. 51, (537) p. 170), though the angle between successive pairs varies, while plants exposed to unilateral illumination are stated by Berthold ((37) p. 573), who made considerable studies on the light-reactions of this species (cf. also (697) p. 545), to develop all the branches

[1] See (37) p. 573, (50) p. 226, (54) p. 51, (93), (357) p. 254, (383) p. 45, (475) p. 200, (476) (as *Pterothamnion*), (478) pp. 374 (as *Pterothamnion*), 378, (537) p. 25, (558) p. 359, (577) p. 137. *Platythamnion* and *Antithamnionella* (437) show essentially the same features.

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in one plane. In this species long shoots also arise adventitiously from the basal cell of a lateral of limited growth.

The early development of *A. plumula* ((129) p. 483, (339) p. 215, (379) p. 15) is like that of *Callithamnion*. A protrusion of the spore becomes cut off as the first rhizoid (fig. 185 D, E, *r*), while the rest divides to produce the erect axis (*e*). According to Berthold ((37) p. 573) the primary axis of *A. cruciatum* soon terminates its growth, while procumbent or ascending branches arise from its base. It can hardly be doubted that the creeping threads of *Antithamnion*, *Spermothamnion*, etc. are always secondary in origin. In *Antithamnion* the creeping threads are attached by unicellular rhizoids, as well as by more elaborate haptera, while in older plants multicellular rhizoids originate from the lower branches of the erect axes; they are of course homologous with the cortical threads of *Callithamnion*. In *A. plumula* ((558) p. 362) some of them develop into runners producing other erect threads.

The interrelationships of the diverse genera so far considered are not altogether clear. Since a uniaxial construction with whorled laterals is characteristic of many of the less specialised Florideae and is also seen in *Crouania* and *Wrangelia* (p. 457) among Ceramiaceae, forms like *Crouania* and *Antithamnion* are probably more primitive than *Callithamnion* and its allies, a point of view which receives considerable support from a consideration of the arrangement of the female reproductive organs (p. 691). Whorled branching of a somewhat different type is also found in *Actinothamnion* ((687) p. 659). *Crouania*, as already noted, altogether conforms to the *Batrachospermum*-type, although the early development is practically identical with that of *Callithamnion* ((129) p. 486, (339) p. 218).

The bilateral branching seen in *Antithamnion* is also characteristic of *Ballia* (p. 744), *Plumaria* (incl. *Euptilota* Cramer non Kütz.), and *Ptilota*, in which, however, the older parts of the thalli show considerable cortication (cf. also *Wrangelia*, p. 459). *Plumaria elegans*[1] ((587) p. 450, (598) p. 5), a small perennial lithophyte, is frequent between tide-levels in the North Atlantic. The thallus shows repeated pinnate branching and, in the younger parts, presents considerable resemblances to an *Antithamnion* (fig. 186 B). The paired laterals arise successively, that first formed (*1–5*) usually developing more strongly than the opposite one. The older ones exhibit a stronger development of the branches of the second order on the abaxial face, the

[1] *Ptilota elegans* Bonnem.; *P. sericea* (Gmel.) Harv. ((276) pl. 191). See (145) p. 6, (380) p. 57, (475) p. 206, (531), (558) p. 352. Naegeli and Cramer described it under the name *Ptilota plumosa*, an altogether different alga, and this was repeated by Oltmanns in the first edition of his book ((500) p. 585), although the error was rectified in the second. There has been much confusion between the two Algae (cf. (357) p. 253).

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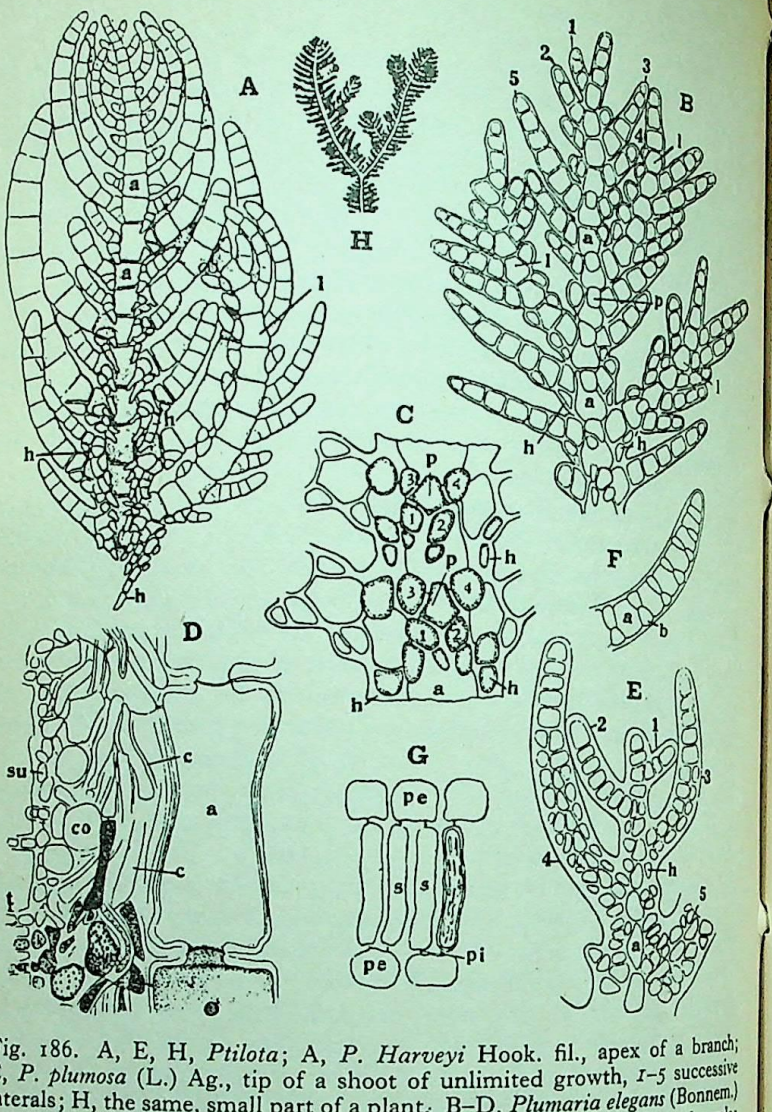

Fig. 186. A, E, H, *Ptilota*; A, *P. Harveyi* Hook. fil., apex of a branch; E, *P. plumosa* (L.) Ag., tip of a shoot of unlimited growth, *1–5* successive laterals; H, the same, small part of a plant. B–D, *Plumaria elegans* (Bonnem.) Schmitz; B, apex of shoot of unlimited growth, *1–5* successive laterals; C, small part enlarged to show manner of cortication; D, longitudinal section through a small part of a mature axis. F, G, *Spyridia filamentosa* (Wulf.) Harv.; F, tip of a young "filament"; G, cortication of axial segments. *a*, axial cells; *b* (in F), cortical cell; *c* (in D), conducting system; *co*, storage-cells; *h*, cortical threads; *l*, laterals of unlimited growth; *p*, cortex-forming cells; *pe* (in G), pericentrals; *pi*, secondary pit-connections; *s* (in G), secondary cortical cells; *su*, surface-layer of thallus; *t*, superficial thread-like outgrowth. (A after Cramer; D after Rosenvinge; F after Taylor; G after Phillips; H after Newton; the rest after Kylin.)

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uppermost ones not uncommonly ending in hairs ((558) p. 353, (559) p. 210). Certain laterals (*l*) develop into long shoots.

The thick cortex enveloping the older axes is produced from two sources. Small cells (fig. 186 B, C, *h*), cut off from the basal cells of the laterals, give rise to cortical threads much as in *Callithamnion*. Apart from this, however, the axial cells (*a*) put out protuberances (*p*) in a plane perpendicular to that in which the main branches of the thallus are formed (cf. *Antithamnion*); each of these cuts off at its four corners (fig. 186 C, *1–4*) small cells which grow out respectively in the upward and downward directions as branched threads covering the axial cells (cf. *Ceramium*). The two kinds of outgrowths gradually produce a thick envelope (fig. 186 D), differentiated into a small-celled photosynthetic layer (*su*), an intermediate storage-layer (*co*) of large cells, and a conducting system (*c*) of long narrow elements surrounding the large axial cells (*a*; (558) p. 354, (744) p. 72). In the older parts certain superficial cells grow out into unbranched threads (*t*) forming a surface felt. The early development is like that of other Ceramiales.

Ptilota plumosa ((276) pl. 80), a robust North Atlantic perennial, often epiphytic on *Laminaria* ((701) p. 70), is very similar in habit and general structure. The laterals (fig. 186 E, *1–5*), here arising from alternate segments of the apical cell,[1] are markedly unequal and the cortex, formed entirely by outgrowths (*h*) from their basal cells ((145) pp. 25, 110,[2] (558) p. 357; cf. also fig. 186 A, *h*), develops at an early stage. It forms an envelope of large storage elements, with one or two layers of small superficial cells, while in the older parts there is a progressive production of hyphae from the former; at first these hyphae surround the axial thread, but later they aggregate in thick bundles and often occupy a large part of the transverse section. The larger axes show some compression.

P. pectinata (Gunn.) Kjellm. (*P. serrata* Kütz. (163)), abundant on the northern coasts of Atlantic America, is essentially similar in structure. See also *P. densa* Ag. (*Pterota densa* Cramer (145) p. 42).

The richly branched tufts of *Ceramium* ((144), (369) p. 174, (513)) are often recognisable by the transverse banding of the younger parts and the tong-like curvature of the forks of the ultimate branches (fig. 187 A, B, D). Each thread is occupied by a row of large cylindrical or barrel-shaped cells (fig. 187 B, I, L, *ac*), the older ones being almost colourless. The rather regular dichotomy ((144) p. 2, (351) p. 343) is initiated by the appearance in the dome-shaped apical cell (fig. 187 C) of two inclined walls which cut out the apicals (*a*) of the forks (fig. 187 D).

At an early stage a series of pericentrals is cut off successively (fig. 187 E, *1*, *2*, *3*, etc.; F, *p*) at the top of each segment, their number

[1] This is not so in all *Ptilotas* (cf. *P. Harveyi*, fig. 186 A). In *Euptilota* ((598) p. 5) the apical cell cuts off somewhat oblique segments ((405) p. 66).
[2] Under the name *Pterota plumosa*.

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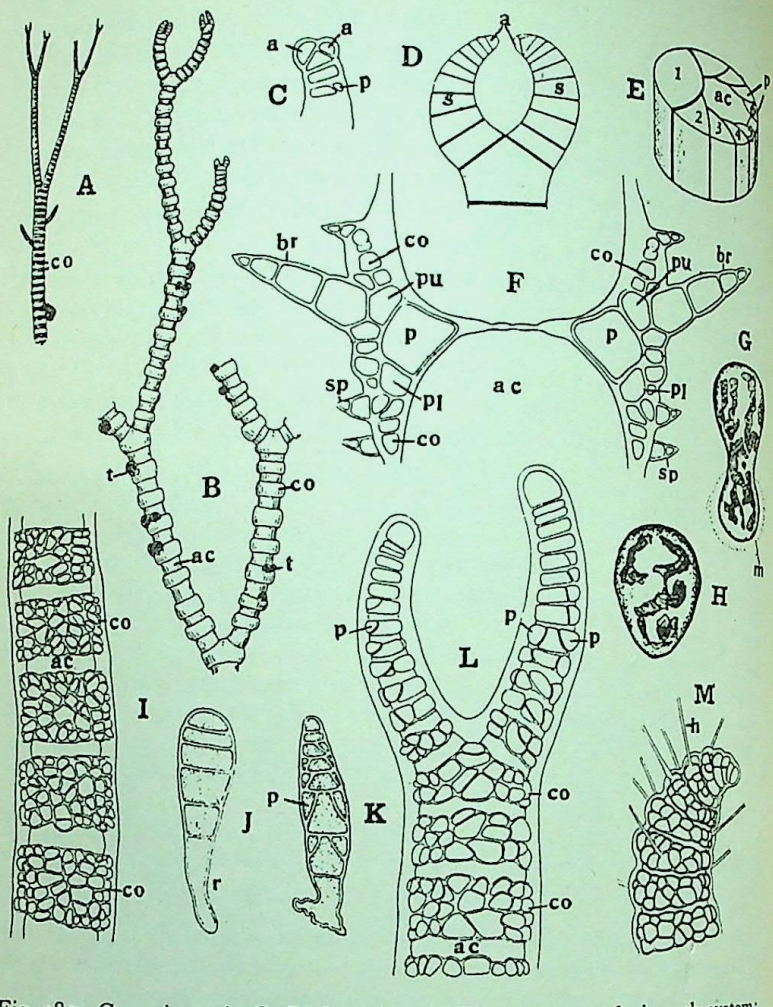

Fig. 187. *Ceramium*. A, *C. Deslongchampii* Chauv., apex of a branch-system; B, *C. fastigiatum* Harv., ditto; C, *C. Deslongchampii*, apical branching; D, diagram of apex; E, diagram to show mode of formation of pericentrals (*1–6*); F, undetermined species, development of cortication and branches (*br*); G, H, J, K, *Ceramium* sp., early stages in development; I, *C. Deslongchampii*, structure of a mature thallus-branch; L, ditto, dichotomy; M, *C. diaphanum* (Lightf.) Roth, apex of thallus-branch with hairs (*h*). *a*, apical cells; *ac*, axial cells; *co*, cortex; *m*, mucilage; *p*, pericentrals; *pl*, lower and *pu*, upper cortical cells; *r*, rhizoid; *s*, segment; *sp*, spine; *t*, tetrasporangia. (A, C–F after Cramer; G, H after Killian; J, K after Pringsheim; the rest after Taylor.)

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being a valuable diagnostic character ((513) p. 87, (524) p. 280). Each cell of the primary cortical band thus produced cuts off four secondary ones (fig. 187 F), two above (*pu*) and two below (*pl*), and these give rise to four branching threads (*co*) which remain closely apposed to the axial cells. In their entirety they gradually form a small-celled cortex which envelopes, not only the upper end of the parent segment, but also extends onto the segment above (fig. 187 I, L, *co*). In some species (e.g. *C. rubrum* (Huds.) J. Ag. (276) pl. 181) the cortical bands of successive segments remain combined to form a uniform investment through which the axial cells are just distinguishable, but in others (*C. diaphanum* (276) pl. 193, *C. strictum* Harv. (276) pl. 334) the lower part of the segment stretches appreciably so that the bands become widely separated (fig. 187 B, I, L) and are visible even to the unaided eye (fig. 187 A). The cortical cells are usually isodiametric or longitudinally elongated, although in *C. transversale* Collins and Hervey ((50) p. 243, (140) p. 145) the lower ones are transversely extended. Hairs ((513) pp. 49, 86, (558) p. 372, (559) p. 208) are frequently present on the younger parts (fig. 187 M, *h*).

The primary cells of the cortical bands are no doubt homologous with those producing branches in other Ceramiaceae, as well as with the pericentrals of Rhodomelaceae. In certain species (e.g. *C. ciliatum* Ducluz. (276) pl. 139), in fact, each of these cells grows out into a short spinous lateral (fig. 187 F, *br*), while in others (e.g. *C. acanthonotum* Carm. (276) pl. 140) only one such branch is produced on each cortical band. The threads arising from the pericentrals are directly comparable to the corticating filaments of *Plumaria*. Their cells may also bear short spinous branches, as in *C. echionotum* J. Ag. ((276) pl. 141; cf. also fig. 187 F, *sp*).

The germlings ((129) p. 488, (173) p. 258, (339) p. 221, (379) p. 18, (531) p. 33, (695) p. 6) are of the usual type (fig. 187 J), except that the spore is attached to the substratum by a cushion of mucilage (fig. 187 G, *m*) which is penetrated by the first rhizoid. Cortex-development commences early (fig. 187 K). The mature tufts are attached ((701) p. 66) by rhizoids originating from the lower axial and cortical cells; their tips form holdfasts and they may occasionally develop cortical bands ((558) p. 372).

Species of *Ceramium* occur abundantly between tide-levels, as well as in deeper water. The Mediterranean *C. radiculosum* Schiller (578) inhabits rivers, especially the estuarine portions. In *C. tenuissimum* (Lyngb.) J. Ag. (*C. nodosum* Harv. (276) pl. 90) and certain other species the cortical bands include colourless refringent cells which contain protein, sometimes in the form of crystalloids ((209) p. 8, (372) p. 9, (381), (384) p. 281, (513) pp. 55, 86, (514) p. 100), which may also occur in the axial cells (fig. 147 M, *cr*).

Several other genera show much the same structure. In *Ceramothamnion* ((140) p. 134, (542), (600), (727) p. 335), which is apparently

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widely distributed in warmer seas, the little-branched erect filaments arise from creeping threads. *Microcladia glandulosa* Grev., a frequent Northern seaweed with distichous branching and slight flattening, has a continuous several-layered cortex. In *Reinboldiella* ((206), (703) p. 35; *Gloeothamnion* (536)) the terete, pinnately branched thalli are completely prostrate; the form and density of arrangement of the cortical cells differ on the two surfaces so that there is some degree of dorsi-ventrality.

The widely distributed perennial seaweed *Spyridia filamentosa* (fig. 188 A; (276) pl. 46) differs considerably from other Ceramiaceae ((2) p. 338, (50) p. 233, (145) p. 75, (520)). The laterals (fig. 188 B, *f*), arising from the first pericentral of each segment, are arranged on a 5/13 spiral,[1]

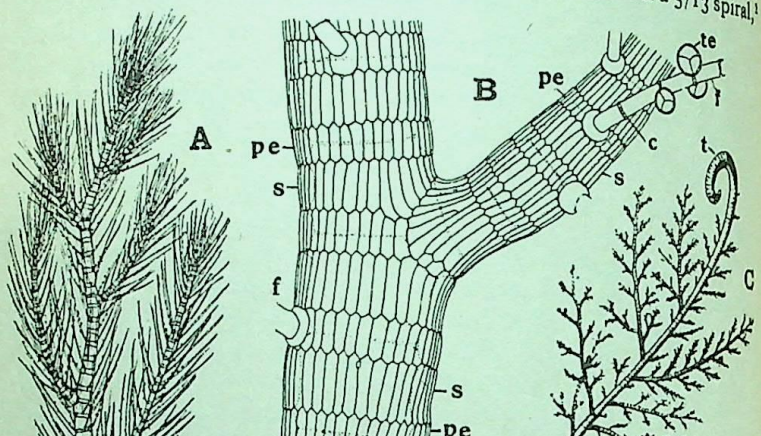

Fig. 188. A, B, *Spyridia filamentosa* (Wulf.) Harv. (after Taylor); A, habit; B, small part of thallus enlarged, with tetrasporangia. C, *S. aculeata* Kütz., with tendril (*t*) (after Nordhausen). *c*, cortex of filament (*f*); *pe*, pericentral cells; *s*, secondary cortical cells; *te*, tetrasporangia.

and most develop into the deciduous photosynthetic "filaments", which occur only on the younger parts (fig. 274 C, *fi*) and also bear the antheridia and sporangia (fig. 188 B, *te*). They consist of about 20 cells which produce a localised cortex (*c*) as in *Ceramium* (cf. also fig. 186 F, *b*); the cortical cells commonly bear long hairs. Each cell of a long axis successively cuts off 14 pericentrals which, as the parent-cell lengthens, remain as a ring at its upper end (figs. 186 G; 188 B, *pe*). Each pericentral gives rise below to two secondary cells (*s*), which lengthen in the same measure as the axial cell and become joined by secondary pit-connections (*pi*) to the underlying ring of pericentrals. According to Taylor ((685) p. 343) the pericentrals subsequently divide longitudinally so that their number is equal to that of the secondary cortical cells (fig. 188 B). The uniformity of the envelope superficially

[1] In the tropical *S. clavata* Kütz. the laterals are distichous ((50) p. 235).

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recalls the appearance of a *Polysiphonia*. The secondary cortical cells are perhaps homologous with the corticating filaments of *Ceramium*, although in *Spyridia* they do not give rise to branched threads. The older parts possess a dense covering of hyphae arising from the cortical cells. The early development is of the usual type ((129) p. 489, (173) p. 257).

(*b*) *Delesseriaceae* ((12), (382), (638) p. 20)

The Delesseriaceae comprise a striking series of often delicate foliose forms[1] in which the thallus commonly shows a development of midribs and lateral veins so as to simulate to a remarkable extent the leaf of a higher plant (fig. 192). They include a considerable number of, frequently perennial, sublittoral forms, which, though widely distributed, probably attain their greatest development in the seas of the Southern Hemisphere ((143) p. 149, (269) p. 470, (382)). The thalli are produced by juxtaposition in one plane of the numerous branches of the axial filament (fig. 189 B), and the greater part of the resulting expanse usually remains one-layered,[1] midribs and veins alone developing a more massive structure. In the Australian *Hemineura frondosa* Harv. ((270) p. 116; *Delesseria frondosa* Hook. f. & Harv. (277) pl. 179), however, most of the frond consists of 3–5 layers of cells.

The cells of the axial row (fig. 189 B, *c*) and of its successive branches are linked by primary pit-connections, while the basal (*b*) and adjacent cells of the laterals, which contribute to the formation of midrib and veins, become joined longitudinally (fig. 193 B, *sp*) by a number of secondary pit-connections ((380) p. 183, (509), (558) pp. 466, 476); such connections also arise between other cells of adjacent rows. In most genera the fronds are capped by a conspicuous apical cell (*a* in figs. 189 B; 191 D) forming a single series of segments, but in most Nitophylleae the apical cell is distinguishable only in younger stages. In the principal axes the segments cut off four pericentrals (fig. 189 E, F), the first two (*lp*) in the plane of branching, the other two (*mp*), which initiate the several-layered ribs, in a plane perpendicular to it. The mode of formation of the pericentrals in Delesseriaceae contrasts with that found in Rhodomelaceae (p. 544) and Dasyaceae. Certain genera (*Apoglossum*, *Delesseria*, *Phycodrys*, Nitophylleae) afford an exception to the strictly apical growth of most Florideae, since they exhibit more or less extensive intercalary division (cf. fig. 193 A).

The apical cell (fig. 189 B, *a*) is very evident in *Hypoglossum Woodwardii*,[2] with rather narrow lanceolate fronds (fig. 189 D). Its

[1] *Pantoneura* ((276) pl. 83, (382) p. 17, (405) p. 47), with a number of species in colder seas, has terete or only slightly flattened thalli, composed of several layers of cells. Various Delesseriaceae found in the Baltic show a great reduction of surface (cf. (426) p. 100 and the literature there cited).

[2] *Delesseria Hypoglossum* (Woodw.) Lamour. ((276) pl. 2). See (12) p. 181, (380) p. 81, (382) p. 9, (472), (475) p. 214, (744) p. 55.

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flat segments (fig. 189 B, *s*) divide into a central (*c*) and two transversely extended pericentral cells (*p*), which function as secondary apical cells. The latter undergo very oblique division to form the

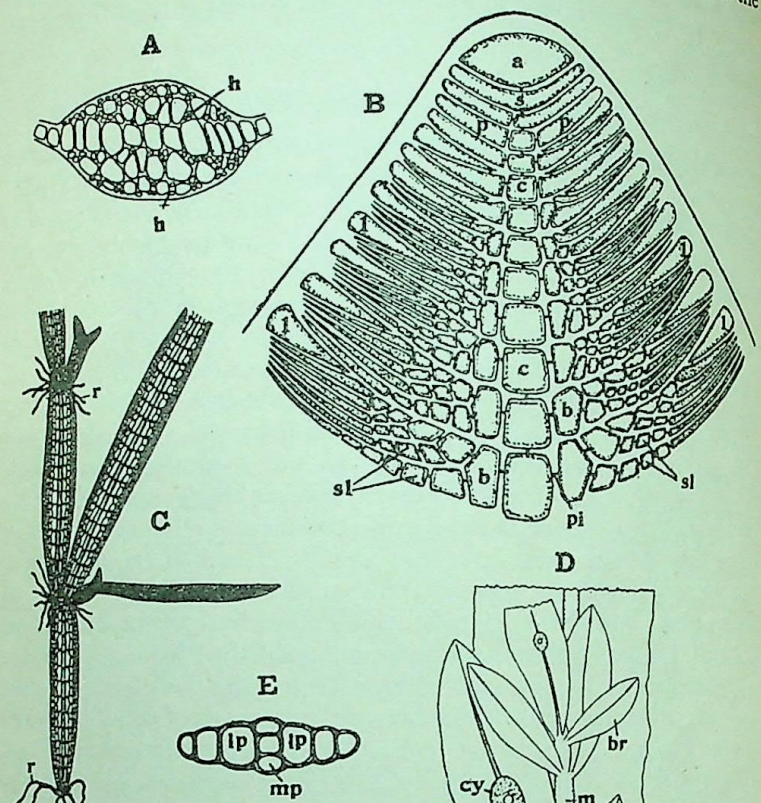

Fig. 189. A, B, D, *Hypoglossum Woodwardii* Kütz. (after Kylin); A, midrib in transverse section; B, apex of thallus; D, part of frond showing mode of branching. C, E, F, *Caloglossa ogaswaerensis* Skuja (after Skuja); C, part of thallus; E, F, transverse sections at different levels. *a*, apical cell; *b*, basal cell of lateral; *br*, branch; *c*, axial thread; *cy*, cystocarp; *h*, hyphae; *l*, apical cells of primary laterals; *lp*, *p*, lateral pericentrals; *m*, midrib; *mp*, median pericentrals; *pi*, pit-connection; *r*, rhizoids; *s*, segment; *sl*, secondary laterals.

pinnately arranged laterals of the first order (*l*, *l*, *l*), which bear all the secondary laterals (*sl*) abaxially. The elongate apicals of the diverse branches all reach the margin of the delicate, though compact, frond.

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A little way behind the apex (fig. 189 B) there is marked elongation of the central cells (*c*) and of the adjacent cells of the primary laterals (*b*), which together form the foundation of the midrib. No other cell-rows are affected so that no veins other than the midrib are present in the mature frond. In the formation of the midrib cells are cut off parallel to the surface (median pericentrals in the case of the axial row, fig. 189 E, F, *mp*), while further thickening is effected by tangential division (fig. 189 A). The subsequent production of a considerable number of narrow hyphae (*h*), between the larger cells composing the midrib, adds to its mechanical strength.

The species of *Caloglossa* ((146), (248) p. 438, (249), (337), (477), (527) p. 45, (646) p. 631), which inhabit tropical streams (313) and especially the brackish estuaries, often accompanying *Catenella*, *Bostrychia*, etc. amid the algal vegetation on the roots of Mangroves ((48) p. 46, (50) p. 341), have a very similar structure. The narrow prostrate thalli show frequent constrictions (fig. 190 C), where forking occurs and bundles of attaching rhizoids (fig. 189 C, *r*) are produced; adventitious branches also arise from the dorsal side of the midrib at the points of forking (fig. 189 C). The apex is commonly inrolled, with the convex surface upwards. The commonest species is *C. Leprieurii* (*Delesseria Leprieurii* Mont. (272) p. 98; *Hypoglossum Leprieurii* Kütz.).

In *Apoglossum ruscifolium*[1] ((12) p. 190, (353) p. 45, (380) p. 83, (484) p. 302) there is more extensive ramification of the cell-rows composing the blade, with adaxial development of the branches of higher orders. Moreover, the cells of the laterals of the first and second orders show marked elongation and form lateral veins which are, however, not visible to the unaided eye. *Grinnellia americana* (fig. 190 A; (12) p. 197, (75), (380) p. 91, (382) p. 20), found on the Atlantic coasts of the United States, is very similar, but only possesses primary veins. The midrib of *Apoglossum* is enveloped in a dense mass of hyphae (fig. 191 C, *h*), but in *Grinnellia* there are only few of these.

In the genera so far considered the branches of the fronds arise from the midrib (fig. 189 D, *br*) and are stated ((558) p. 474), in *Hypoglossum* and *Apoglossum*, to develop endogenously from the central cells (cf. however (380) p. 85). In *Membranoptera alata*[2] (*Delesseria alata* (Huds.) Lamour. (276) pl. 247), on the other hand, the copious branching is due to the further development of the apical cell of a lateral of the first order (figs. 190 D; 192 B) and often results in apparent dichotomy; tufts of adventitious fronds (fig. 190 D, *a*), some of which bear reproductive organs ((558) p. 484), arise in the angles between the branches. *M. alata* is a northern form, with a conspicuous midrib (fig. 192 B) and narrow wings traversed by lateral veins.

[1] *Delesseria ruscifolia* (Turn.) Lamour. ((276) pl. 26).

[2] See (380) p. 108, (382) p. 14, (519) p. 183, (558) p. 481, (742) pp. 31, 64, (744) p. 62.

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The handsome *Delesseria sanguinea*[1] (*Hydrolapathum sanguineum* J. Ag.), sometimes called the "dock-leaved *Delesseria*" and found in shaded situations between tide-levels, as well as in deeper water, has

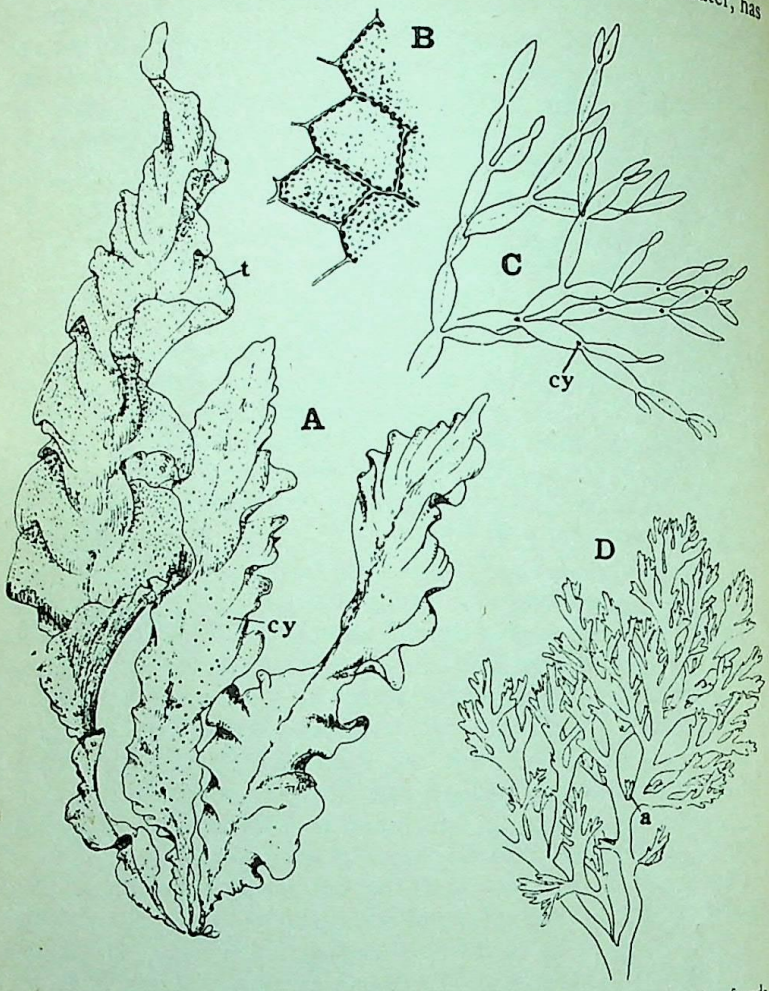

Fig. 190. A, B, *Grinnellia americana* (C. Ag.) Harv.; A, habit showing fronds with tetraspores (*t*) and cystocarps (*cy*); B, a few cells in surface-view. C, *Caloglossa Leprieurii* (Mont.) J. Ag., part of a plant with cystocarps (*cy*). D, *Membranoptera alata* (Huds.) Stackh., habit. *a*, adventitious fronds. (All after Taylor.)

fronds (fig. 192 A) which may reach a length of 25 cm., with conspicuous side-veins produced from the primary laterals; secondary veins, formed from the cell-rows of the second order, are usually only apparent under the microscope. As in *Hypoglossum*, laterals of higher

[1] See (276) pl. 151, (353) p. 41, (369) p. 136, (380) p. 92, (519) p. 177, (530), (558) p. 475, (744) p. 57; and for other species (638) p. 21.

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orders for the most part arise abaxially. Both in *Apoglossum* and *Delesseria* intercalary divisions occur in all but the axial cell-row ((380) p. 93).

The robust midrib develops as in *Hypoglossum*, but the basal cells of the primary laterals (fig. 191 B, *b*) divide transversely so that they are only half as long as the central cells. The surface layer of the mid-

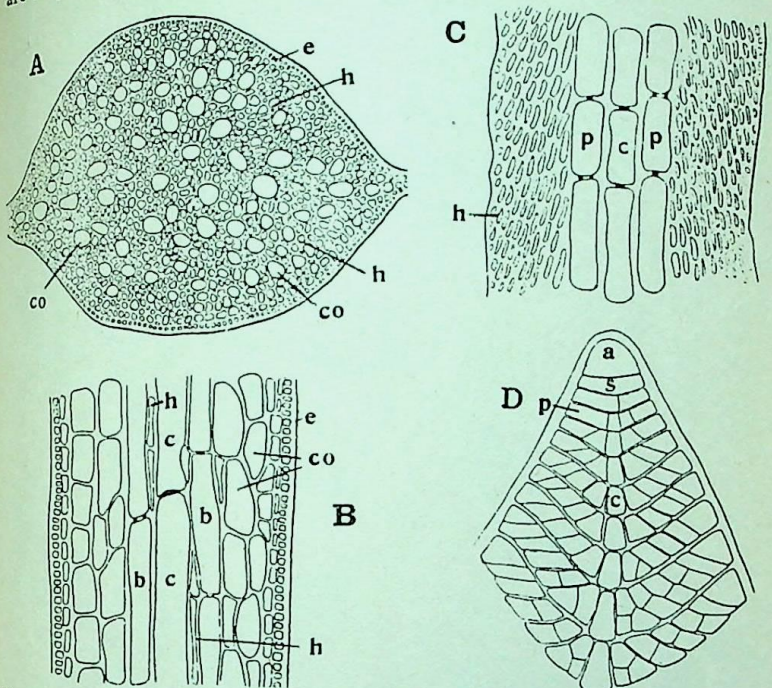

Fig. 191. A, B, D, *Delesseria sanguinea* Lamour.; A, transverse section of old midrib; B, longitudinal section of midrib; D, apex of frond. C, *Apoglossum ruscifolium* (Turn.) J. Ag., longitudinal section of midrib. *a*, apical cell; *b*, elongate cells around axial thread; *c*, axial thread; *co*, cortical cells; *e*, surface-layer of midrib; *h*, hyphae; *p*, pericentrals; *s*, segment. (D after Rosenvinge; the rest after Kylin.)

rib remains meristematic for some time and forms a relatively wide zone of large elements (*co*) bounded by a small-celled superficial layer (*e*); in the older ribs (fig. 191 A) the larger cells (*co*) appear isolated amid a plexus of narrow branched hyphae (*h*; (744) p. 60), which appear to serve for storage. The veins of the first order develop in an analogous manner, while the secondary ones are at best only three-layered.

The branches again develop from the midrib,[1] for the most part in autumn and winter, and appear to originate from surface-cells. The

[1] Rosenvinge ((558) p. 476), however, describes instances in which branching is effected as in *Membranoptera*.

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wings of the parent-frond gradually wear away, leaving the persistent midrib ((362) p. 445), the cells of which contain large quantities of starch ((353) p. 41) which decrease as the new blades develop. The attachment of the young fronds to the parent is strengthened by hyphae that penetrate into the midrib ((558) p. 477).

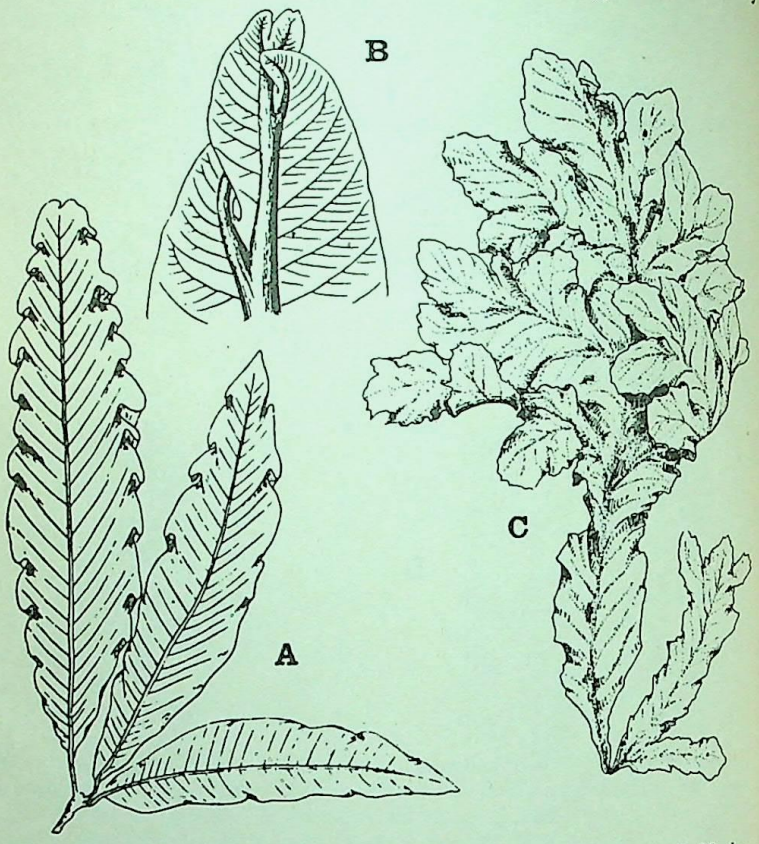

Fig. 192. A, *Delesseria sanguinea* Lamour., habit (after Newton). B, *Membranoptera alata* (Huds.) Stackh., apex of a frond (after Rosenvinge). C, *Phycodrys rubens* (Huds.) Batt., habit (after Taylor).

The Delesserieae, comprising the genera hitherto considered, differ vegetatively from the Nitophylleae in the possession of prominent apical cells and the absence of intercalary division in the axial cells. The widely distributed *Phycodrys rubens* (Huds.) Batt.[1] (fig. 192 C), though a member of Nitophylleae, shows considerable resemblance to *Delesseria*. Branching of the cell-rows may take place to the fifth degree. The main apical cell (fig. 193 A, *ac*) is not very conspicuous

[1] *P. sinuosa* (Huds.) Kütz.; *Delesseria sinuosa* (Good. & Wood.) Lam. ((276) pl. 259). This has been repeatedly investigated; see (380) p. 67, (483) p. 193, (519) p. 189, (558) p. 467, (590) p. 113, (742) pp. 30, 51, (744) p. 65; cf. also (637). Several of the earlier accounts are not altogether accurate (cf. (380)).

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and intercalary division (see the cells marked *i*) occurs both in the axial and other cell-rows. As in *Apoglossum* and *Delesseria*, it is always the lower cell formed by such division (*2*, *3*, *4*; *a*, *b*, *c*) that retains the primary pit-connection with the lateral cell-row (*s1*, *s2*, *s3*), while the upper cells give rise to accessory cell-rows (*r* in fig. 193 A).

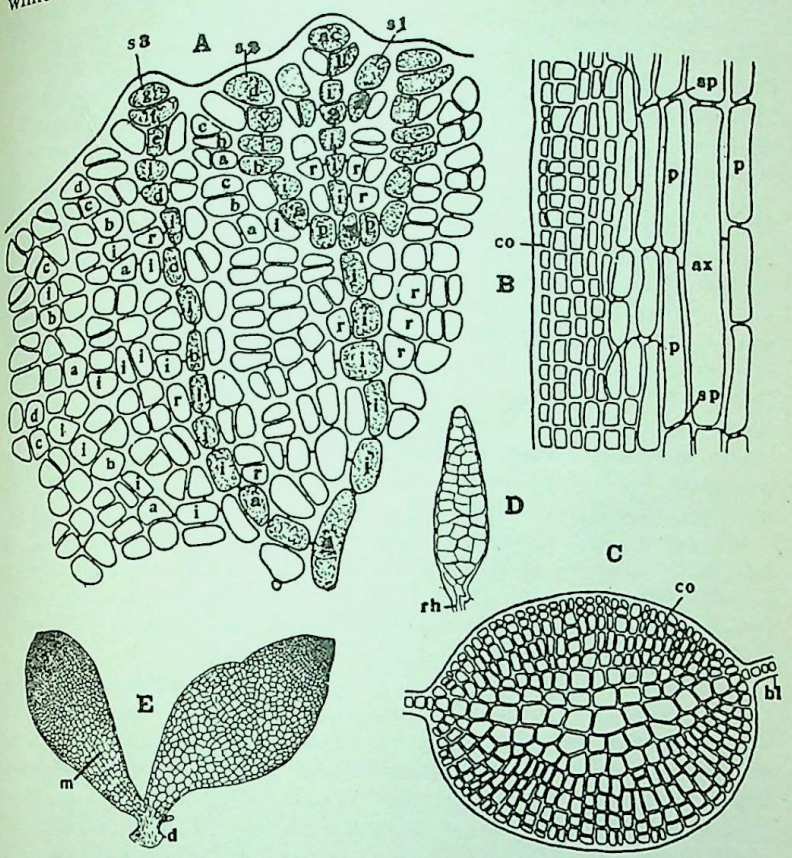

Fig. 193. *Phycodrys rubens* (Huds.) Batt. A, apex of a frond in surface-view; *1*, *2*, *3*, *4*, cells of axial strand; *s1*, *s2*, *s3*, apical cells of primary laterals; *a*, *b*, *c*, *d*, etc., successive cells of primary laterals; *i*, cells formed by intercalary division; *r*, cells of branches arising from these cells. Axial row and primary laterals shaded. B, longitudinal and C, transverse sections of midrib. D, germling. E, older stage. *ac*, apical cell; *ax*, axial thread; *bl*, wing of frond; *co*, cortex; *d* (in E), attaching disc; *m*, midrib; *p*, pericentrals; *rh*, rhizoids; *sp*, secondary pit-connection. (D, E after Rosenvinge; the rest after Kylin.)

The frequent intercalary division, with production of accessory laterals, makes the detailed structure of the fronds more difficult to decipher.

The lobing of the fronds of *Phycodrys* (fig. 192 C) is due to outgrowth of primary laterals (cf. *Membranoptera*), while a similar activity on the

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part of those of the second order results in the marginal pinnules on the lobes. There are obvious primary and secondary veins, while those of the third order are only evident under the microscope. The midribs and veins develop like those of *Delesseria*, but no hyphae are produced (fig. 193 B, C). Branching takes place from the midrib and in older plants the fronds arise from a robust axis constituted by the primary midrib; occasionally, however, a lobe of the blade develops vigorously and leads to a kind of forking. Wille ((744) p. 67) describes the development, from the base of the stalk (midrib), of thread-like runners giving rise at intervals to secondary fronds, many of which remain arrested. A prominent apical cell is also met with in *Haraldia* (203) in which the vegetative fronds are monostromatic and without veins.

In other Nitophylleae apical cells and the construction of the fronds from a coalescent branch-system are still more difficult to decipher. Most of the seaweeds in question were formerly grouped in *Nitophyllum*, though many are now referred to distinct genera. All are characterised by marginal branching and the absence of a distinct midrib. In its present limits *Nitophyllum* ((382) p. 69, (396) p. 4) includes species with foliose thalli, in which the older parts consist of several layers, while the younger are single-layered; there is sometimes a short basal stalk, composed of small regularly arranged cells (fig. 194 F). Veins are either completely lacking—e.g. the widely distributed *N. punctatum* ((276) pl. 202)—or occur only at the base of the thallus (*N. Bonnemaisonii* Grev. (276) pl. 23). In the mature plant there are no evident apical cells (fig. 194 H), growth being effected by marginal, as well as by irregular intercalary, division just within the margin ((483) p. 184). In *N. versicolor* Harv. ((276) pl. 9) the tips and margins of the fronds often display curious thickenings which are suspected of playing a rôle in vegetative propagation ((329), (594) p. 228).

In *Polyneura* (fig. 194 A; (12) p. 51, (382) p. 33) and *Cryptopleura* (fig. 195 A; (12) p. 60, (382) p. 86) veins form an obvious anastomosing or palmate system in the older parts, while in the younger one-layered portions they are only recognisable under the microscope. *Polyneura Gmelini* (Grev.) Kyl. (*Nitophyllum Gmelini* Grev. (276) pl. 235) and *Cryptopleura lacerata* (*N. laceratum* Grev. (276) pl. 267) are frequent, North Temperate, sublittoral forms. In the latter (fig. 195 B, C, *s*) there are evident two-sided apical cells ((479) p. 562, (483) p. 203) which are also recognisable in the smaller lobes of *Myriogramme* ((382) p. 55), in which the older parts are several-layered. Younger and older apices of *Polyneura* are shown in fig. 194 B and C.

Acrosorium ((382) p. 76, (488) p. 26), with delicate, richly lobed fronds (fig. 195 D), possesses only microscopic veins. *A. uncinatum* (J. Ag.) Kyl. (*Nitophyllum uncinatum* (Turn.) J. Ag.) is widely distributed in warmer seas. The frequent *A. reptans* (Crouan) Kyl. (*N. reptans* Crouan), with completely prostrate fronds, is probably a stage of *Cryptopleura lacerata* ((89) p. 187, (153), (435)).

The early development of Delesseriaceae ((129) p. 500, (379) p. 21, (483) p. 185) differs somewhat from that of other Ceramiales. In

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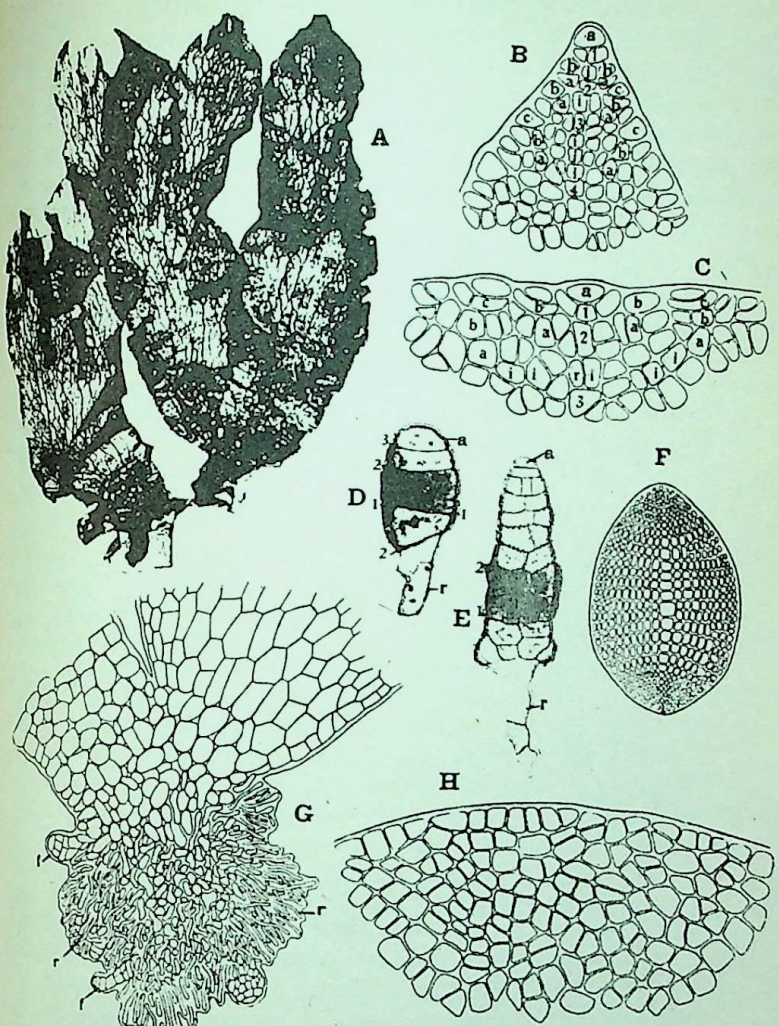

Fig. 194. A–C, F, *Polyneura latissima* (Harv.) Kyl.; A, habit; B, C, apices of thallus-segments; F, transverse section of stalk. D, E, G, H, *Nitophyllum punctatum* (Stackh.) Grev.; D, E, early stages in development, *1–3* the successive septa; G, basal part of older germling; H, apex of mature thallus in surface-view. In B and C *1*, *2*, *3*, etc., cells of the axial row; *a*, *b*, *c*, etc. (small letters), cells of laterals of first order; *i*, cells formed by intercalary division. *a*, apical cells; *f*, adventitious fronds; *r*, rhizoids. (A after Nott; D, E, G after Nienburg; the rest after Kylin.)

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Nitophyllum the broadened spore divides transversely (fig. 194 D, *1–3*) into a row of six cells, the two uppermost of which form the mature thallus, the top one functioning as an apical cell (*a*). The lower part of the germling develops into a mainly monostromatic expanse (fig. 194 G), which is attached by numerous rhizoids (*r*) and gives rise to adventitious fronds (*f*). The early stages are similar in *Apoglossum ruscifolium* (484), which is stated ((357) p. 256, (362) p. 445) to complete its whole development in a few weeks. According to Chemin the segmentation is in neither instance as regular as described by Nienburg. The apical cell of *Nitophyllum* soon ceases to function as the apex broadens and marginal growth sets in.

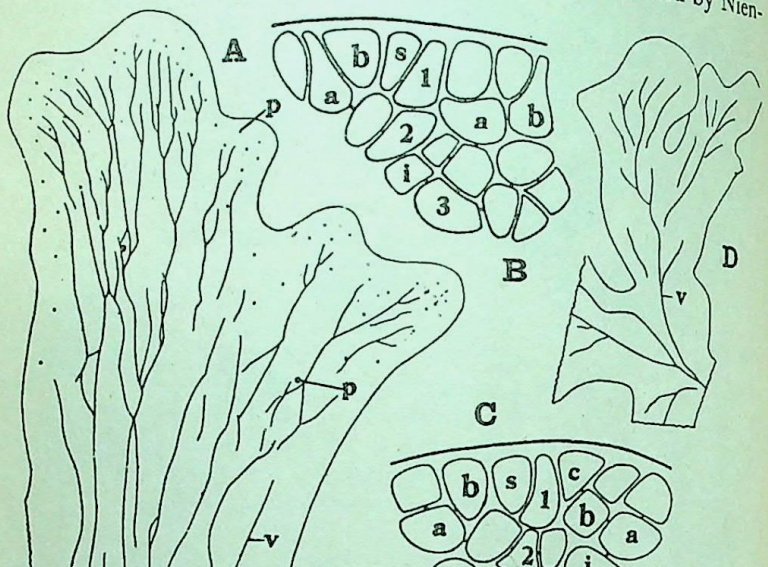

Fig. 195. A–C, *Cryptopleura lacerata* (Gmel.) Kütz.; A, part of a frond, showing the veins; B, C, marginal parts of fronds. D, *Acrosorium venulosum* (Zanard.) Kyl., part of frond. *1–3*, cells of axial row; *a–c*, cells of primary laterals; *i*, cells formed by intercalary division; *p*, procarps; *s*, apical cell; *v*, veins. (All after Kylin.)

The germling of *Phycodrys* ((558) pp. 466, 471) is like a young *Nitophyllum*, consisting of a one-layered expanse devoid of a midrib and showing plentiful intercalary division (fig. 193 D); the mature fronds (fig. 193 E, *m*) arise adventitiously from its stalk. The young plants of *Delesseria sanguinea* ((558) p. 478), on the other hand, have a distinct midrib, but at an early stage again produce adventitious fronds from the basal stalk. The discoid attachments of Delesseriaceae (fig. 193 E, *d*) consist of numerous, closely compacted multicellular rhizoids.

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In spite of a certain gradation, the contrast presented by the extreme members of Delesserieae and Nitophylleae is evident from a comparison of *Hypoglossum* and *Nitophyllum*. Both, in their respective ways, appear highly specialised, and their relation to one another is not clear. A study of the early development in a wide range of forms might help to elucidate it.[1]

The Delesseriaceae also include several genera with a net-like thallus. That of *Claudea* ((2) p. 1272, (3), (5) p. 27, (268), (271) p. 145, (508)) appears as a network with rectangular meshes and constituted by numerous narrow fronds, which are placed edgewise and perpendicular to one another (fig. 196 A); they have much the same structure as in *Hypoglossum*. The diverse parts of the reticulum originate by unilateral branching from the adaxial surface of the midrib of the next younger generation (fig. 196 B). The secondary fronds (*sb1*) arising from the primary one grow to a considerable length, while the tertiary ones (*tb*) usually consist of only 5–8 segments and become joined at their tips (*a*) to the lower surface of the secondary blade (*sb2*) immediately above. The secondary fronds thus form the long bars and the tertiary ones the perpendicular cross-bars of the net.

The base of the primary frond soon becomes invested by a thick cortex and constitutes a stalk. The primary and secondary blades develop a cortex over their entire surface, while in the tertiary ones, except in fertile plants, only the midrib is corticated. *Claudea* differs from other Delesserieae in the fact that two pericentrals, situated one in front of the other (fig. 196 B, *vp1*, *vp2*), are cut off successively on the adaxial (ventral) side of the segments, the larger posterior one (*vp2*) growing out into a daughter-blade (*tb*). Between the apical cells (*a*) of the tertiary blades (*tb*) and the dorsal pericentrals (*dp*) of the secondary blade (*sb2*) upon which they abut, secondary pit-connections (*pi*) are established; later other connections are formed. Enlargement of the cells results in increase in size of the meshes of the net (cf. the lower part of fig. 196 B), but growth of the primary and secondary blades terminates after they have reached a certain length. Occasional tertiary blades, however, develop vigorously and produce quaternary blades which become linked with the dorsal surface of the blade immediately above. This results in forking and, since secondary fronds develop also from surface-cells of the stalk, older plants may exhibit considerable branching (fig. 196 A). The nets are attached both basally and at other points by septate rhizoids.

C. multifida is widely distributed in South India and Ceylon, while *C. elegans* Lamour. ((277) pl. I) is apparently confined to Australia. The sessile net-like thalli of *Vanvoorstia* ((2) p. 1268, (271) p. 144, (508) p. 31), recorded from various parts of the Indian Ocean and Japan, are formed in essentially the same way (cf. fig. 196 C), but more numerous branchings occur and all the fronds remain uncorticated. Papenfuss regards

[1] The affinity of Delesseriaceae with other Ceramiales is discussed on p. 720.

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these genera as closely related to *Caloglossa*. A similar reticulate thallus is found in the Japanese *Implicaria* (299), but here the successive terete axes produce pinnately arranged branches.

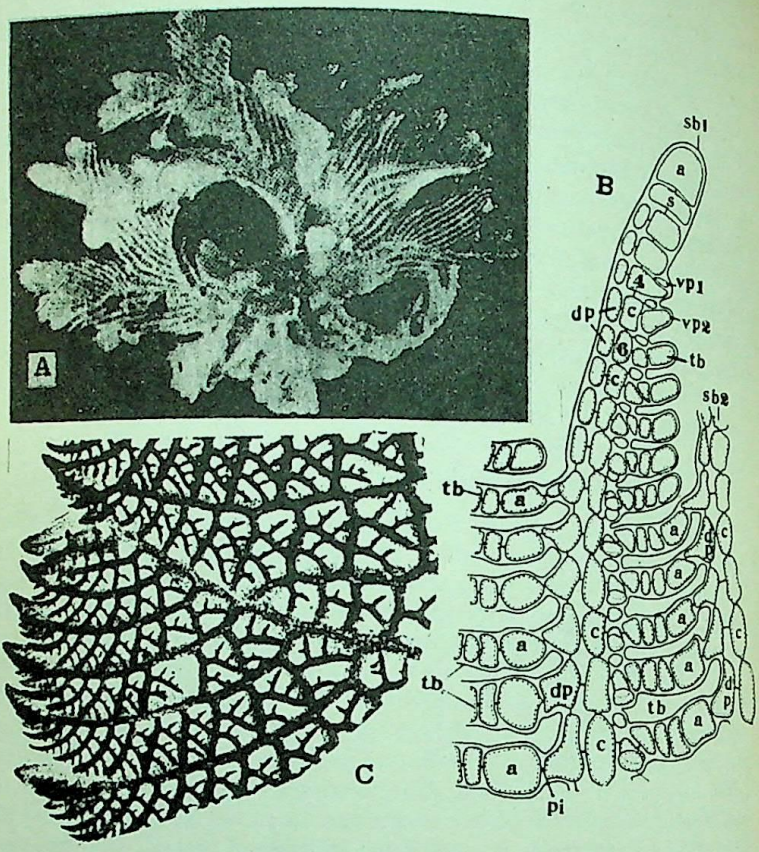

Fig. 196. A, B, *Claudea multifida* Harv.; A, habit; B, optical median longitudinal section of a secondary blade (*sb 1*) showing the origin of tertiary blades (*tb*), the fusion with the adjacent secondary blade (*sb 2*) and the early stages in the formation of the interstices of the net. *a*, apical cells; *c*, axial cells of secondary blades; *dp*, dorsal pericentrals; *pi*, secondary pit-connection; *s*, segment; *tb*, tertiary blades; *vp 1*, *vp 2*, ventral pericentrals. C, *Vanvoorstia spectabilis* Harv., portion of thallus. (All after Papenfuss.)

A different type of reticulate thallus is found among Nitophylleae in the genus *Martensia*, species of which are known from South Africa, India, and Australia ((2) p. 825, (50) p. 348, (271) p. 145, (277) pl 8, (663)). The lower, first formed, part of the thallus (fig. 197 B) is here a continuous expanse,[1] which is sometimes stalked (fig. 197 C),

[1] The early development of the adventitious shoots, which arise from the basal parts of older plants, follows much the same sequence as in Nitophylleae; the primary apical growth becomes altogether obscured as abundant intercalary division sets in.

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while the older part (fig. 197 A, C) is constituted by a network (*n*) of diverse width. The latter (fig. 197 E) consists of radiating lamellae (*l*), joined by numerous tangential connections (*c*). The lamellae

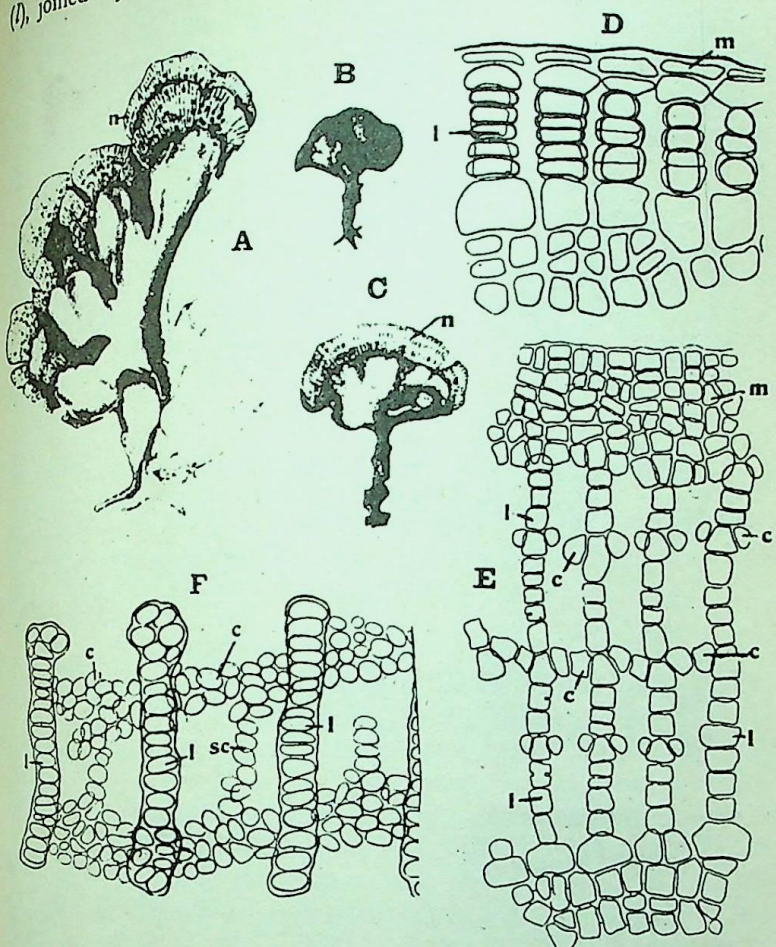

Fig. 197. *Martensia fragilis* Harv. A, habit showing folded thallus. B, young plant. C, older stage, with net-formation commencing. D, edge of thallus in surface-view showing commencement of formation of longitudinal lamellae (*l*). E, the same at a later stage showing development of cross-connections (*c*). F, transverse (tangential) section in region of net. *c*, tangential cross-connections between the lamellae; *l*, lamellae; *m*, entire margin of thallus; *n*, net; *sc*, secondary connections. (All after Svedelius.)

originate just behind the edge of the young thallus (fig. 197 D) by abundant and long-continued intercalary division of the intramarginal cells and lateral separation of the rows (*l*) thus formed; the marginal cells (*m*), however, remain in contact and divide to form the several-layered edge of the net (fig. 197 E, *m*). The cells of the sepa-

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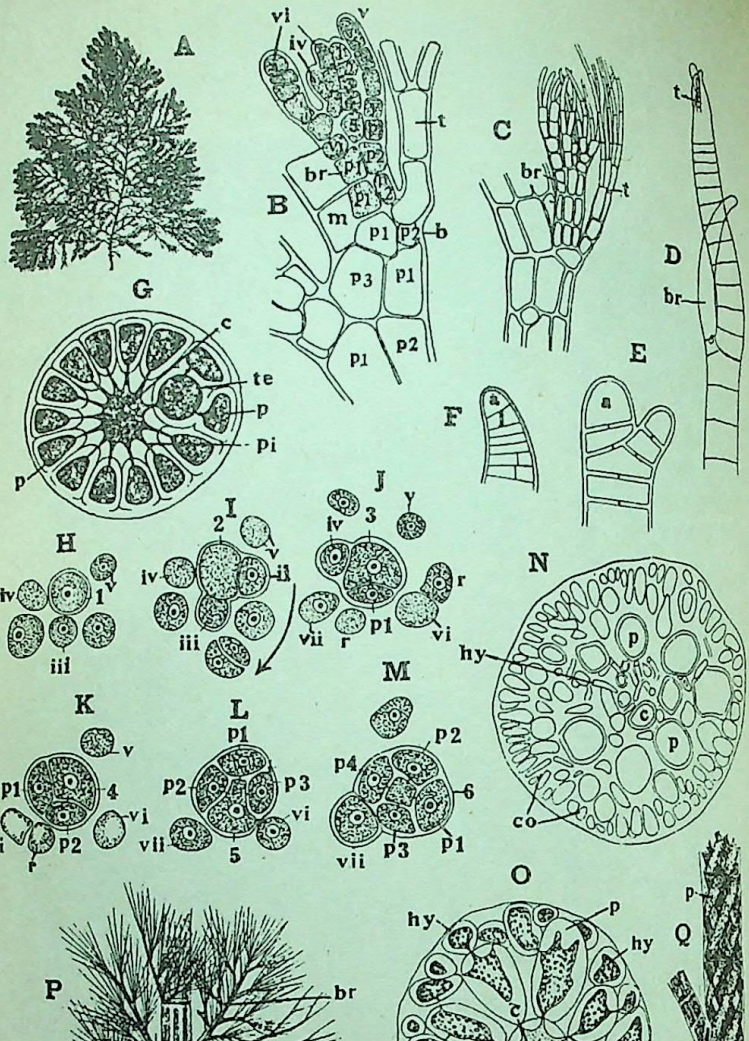

Fig. 198. A–O, Q, R, *Polysiphonia*; A, *P. nigrescens* (Huds.) Grev.; B, C, H–M, *P. violacea* (Roth) Grev.; D, F, *P. variegata* (C. Ag.) Zan.; G, R, *P. fastigiata* (Roth) Grev.; N, O, *P. Brodiaei* Grev.; Q, *P. spiralis* Batten. A, habit; B, development of lateral of unlimited growth on trichoblast (*t*); *iv*, *v*, *vi*, branches; *1*, *2*, *3*, etc., cells of main axis of branch; C, older branch (*br*) on trichoblast (*t*); D, apex showing curvature of branches; E, diagram to show branch-formation (in a *Bostrychia*); F, apical segmentation; G, transverse section showing developing tetrasporangium (*te*); H–M, transverse

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rating rows within the margin divide parallel to the surface to produce vertical lamellae, which remain monostromatic, except at their edges (fig. 197 F, *l*). Cross-connections (fig. 197 E, *c*) are formed between adjacent lamellae by the outgrowth of processes which fuse and ultimately come to consist of several rows of cells (fig. 197 F, *c*). The cross-connections arise successively, the later-formed ones about midway between the earlier ones. The older nets often exhibit branching of the cross-connections, which may thus become linked with one another (fig. 197 F, *sc*).

Net-formation may commence early (*M. flabelliformis* Harv.) or only at a later stage (*M. fragilis*, *M. denticulata* Harv. ((277) pl. 127). In *M. fragilis* (fig. 197 A) the numerous lobes exhibit a cornet-like inrolling, while the entire portions of adjacent fronds become firmly joined by thick haptera so that compact cushions are formed. In *M. denticulata* and *M. pavonia* J. G. Ag. belts of compact and reticulate tissue alternate.

(*c*) *Rhodomelaceae*

The members of this large family, monographed by Falkenberg (192), show a varied and in part complex morphology. All are characterised by the basic polysiphonous structure, as well as by the usual production of laterals of two different types (ordinary branches and trichoblasts). Unicellular hairs are lacking ((558) p. 463).

(i) *Rhodomelaceae with Radial Construction*

Polysiphonieae and Lophothalieae. *Polysiphonia*,[1] readily recognised by the arrangement of its cells in tiers, illustrates all the main features of the family. *Brongniartella*[2] is essentially similar. The dome-shaped apical cell (fig. 198 F, *a*) forms a single series of segments; those which produce laterals (*l*) are larger than the others and are cut off by oblique walls.[3] As in all Rhodomelaceae (cf. figs. 200 B; 207 B), the initial of the lateral is cut off on the higher side *before* the segment divides longitudinally into central and pericentral cells (cf. fig. 198 I, *iii*).

[1] See (25), (192) p. 111, (350) p. 102, (473), (549), (558) p. 406, (750), (780).
[2] See (192) p. 542, (350) p. 106, (547) p. 22, (549) p. 33, (558) p. 445, (592) p. 217.
[3] See (38), (192) p. 38, (380) p. 116, (399), (547) p. 10, (549), (556) p. 350, (710).

sections through successive segments (*1–6*) showing sequence of formation of pericentrals (*p1*, *p2*, *p3*, *p4*) and of trichoblasts (*iii*, *iv*, *v*, etc.); N, transverse section of an old and O, of a younger thread; Q, small part of thread showing spirally twisted pericentrals; R, scheme of pericentral-formation. P, *Brongniartella byssoides* (Good. & Wood.) Schmitz, part of shoot-system. *a*, apical cell; *b*, basal cell of trichoblast; *br*, branches of unlimited growth; *c*, axial cells; *co*, cortex; *hy*, hyphae; *l*, segment which will form a lateral; *m*, cell of main axis; *p*, pericentrals; *pi*, pit-connections; *r*, *t*, trichoblasts. (A after Taylor; C after Boergesen; D, F after Berthold; E, G, P, R after Falkenberg; N, O after Rosenvinge; Q after Batten; the rest after Rosenberg.)

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The laterals (fig. 198 H–M, *ii–vii*; here trichoblasts, cf. below) are formed in spiral succession (556, 607). According to Rosenvinge (550) p. 6) the nucleus moves to the side on which the lateral will arise before the segment is separated from the apical cell, while the ingrowing septum originates on the opposite side. The laterals and parent-axes often exhibit temporary curvatures towards one another (fig. 198 D; (37) p. 623, (192) p. 43).

The mode of formation of the pericentrals is distinctive of all Rhodomelaceae. They invariably develop successively (fig. 198 J–M, *p1–p4*; R), the first one being cut off beneath the lateral, although there is commonly a subsequent displacement to the left in the direction of the spiral (cf. fig. 198 L, M) so that the lateral appears above another pericentral or located between two of them. In segments which produce no laterals, the first-formed pericentral occupies the same position as in the next upper segment bearing a lateral. The number of pericentrals varies between 4 and 20 and is usually constant, especially in species with few pericentrals. When there are four (*P. violacea*, fig. 198 K–M; *P. elongata*), the second (*p2*) and third (*p3*) are cut off on either side of the first, and the fourth (*p4*) on the side opposite to the lateral; when they are more numerous, they develop in the sequence shown in fig. 198 R.

The pericentrals of *Polysiphonia* and *Brongniartella* (fig. 198 P) occupy the whole length of the segment and are usually broader than the central cell (fig. 198 G, O), which shimmers through the enveloping "siphons". They are homologous with the primary cortical cells of *Ceramium* (p. 527) and represent potential branches; in *Chondria* (p. 556), in fact, they lengthen to form the elongate laterals composing the thallus. Primary pit-connections occur only between successive central cells and between the latter and their pericentrals (fig. 198 G, O, *pi*). Secondary connections (551) are later formed between overlying pericentrals (cf. p. 449 and fig. 147 C) and in some species (*P. elongata*) several may develop ((558) pp. 416, 465). The central cells usually remain uninucleate.

In many species the erect threads produce laterals of two kinds, viz. some which are polysiphonous like the parent axis and some which develop into branched, uniseriate structures of limited growth, usually deciduous at an early stage (fig. 198 B, C, *t*). The latter are the *trichoblasts*[1] ((192) p. 62, (557) p. 440, (558) p. 462) found in many Rhodomelaceae. They are ordinarily composed of colourless cells containing small leucoplasts,[2] but in *Brongniartella* (fig. 198 P) the cells of the long-lived trichoblasts (*t*) contain chromatophores and

[1] "Leaves" of Falkenberg and others; "hair-shoots" ("Haartriebe") of Oltmanns.

[2] Rosenvinge ((557) p. 446, (558) p. 463) records chromatophores of a light rose colour in the trichoblasts of individuals of *Polysiphonia* gathered in spring or from considerable depths.

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play an important rôle in photosynthesis ((557) p. 469). Although many of the trichoblasts fulfil vegetative functions only, they usually bear the sex organs (p. 701), and in some species of *Polysiphonia* (*P. urceolata* (Lightf.) Grev.; *P. fastigiata*) such fertile trichoblasts may be the only ones present ((557) p. 449).

Apart from the first, each segment of the trichoblast generally produces a lateral (fig. 198 P) which often develops as vigorously as the part beyond, resulting in pseudo-dichotomous branching. In *Polysiphonia* and *Brongniartella* the trichoblasts are disposed in a spiral, which almost invariably turns to the left (fig. 198 H–L) and the first branch of the trichoblast (*r* in fig. 198 J) is always situated on the anodic side (i.e. to the right, cf. (549, 550)). Trichoblasts are either distributed over considerable parts of the plant or restricted to certain regions. Their morphological status and function are considered below (p. 549).

The ordinary polysiphonous branches either arise direct (fig. 198 D, *br*) and in spiral succession from the parent-axis, replacing one of the trichoblasts when these are present, or they originate from the upper surface of the basal segment of a trichoblast. The former condition is seen in *P. urceolata*, *P. elongata*, *P. nigrescens*, etc. In the basal segment of the branch the first pericentral is formed abaxially, above the first-formed one of the parent-segment, but the production of pericentrals is suppressed on the opposite side, where the branch-segment is in contact with the axis ((547) p. 11, (549) p. 25). The supra-basal segment, which bears no lateral, has the normal number of pericentrals with the same orientation.

The origin of branches from trichoblasts ((141) p. 127, (350) p. 102, (549) p. 36, (557) p. 467) is more frequent. In *Polysiphonia* (*P. decipiens*, *P. violacea*, *P. Brodiaei*, etc.) they arise almost simultaneously with the parent-trichoblast (fig. 198 B, C, *br*), whereas in *Brongniartella* (fig. 198 P, *br*) they only develop when the latter is almost mature. In a *Polysiphonia* the basal segment of the few-celled trichoblast puts out a protrusion which is cut off by an oblique septum and becomes the apical cell of the branch. After this has undergone a number of divisions, the basal segment of the trichoblast (fig. 198 B, *b*) cuts off two pericentrals (*p1*, *p2*) abaxially, to right and left of the median line; sometimes a third pericentral is formed (*P. Brodiaei* (547) p. 18) Until the branch itself commences to form trichoblasts (fig. 198 B), the first pericentrals (*p1*) of its segments lie in a straight line with the first (left-hand) pericentral of the basal segment of the trichoblast. During the further development of the branch the upper part of the trichoblast becomes displaced so that the former appears as a direct outgrowth from the main axis. In origin the branch is, however, obviously a lateral outgrowth of the trichoblast-rudiment, and it cannot justifiably be interpreted as axillary (cf. (192) p. 65, (350) p. 100) to the trichoblast.

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The normal acropetally formed branches are sometimes supplemented by adventitious ones which originate from the basal cells of trichoblasts that have been shed; this is the rule in *P. violacea* ((558) p. 424). Adventitious branches may also arise in this way in species in which the normal branches are not formed on the trichoblasts. Thus, according to Rosenvinge ((558) p. 416), the new shoots of *P. elongata* that appear in spring originate partly from the remains of the axes of the previous season and partly from the basal cells of their trichoblasts, and the same is recorded for *P. nigrescens* ((192) p. 130, (447), (549) p. 3). Rosenvinge suggests that the normal branch-formation on trichoblasts has resulted from this tendency to form adventitious branches upon them (cf. also (547) p. 16).

In many *Polysiphonias* (*P. urceolata*, *P. nigrescens*), as well as in *Brongniartella*, some of the polysiphonous axes creep over the substratum ((25) p. 276, (192) p. 129, (357) p. 253, (549) p. 22, (558) p. 407), to which they are firmly anchored by thick-walled, often richly lobed, unicellular rhizoids arising from the peripheral cells (fig. 199 I, *r*). The creeping branches, which constitute a means of perennation ((353) p. 51), lack trichoblasts and are secondary in origin, arising endogenously from the central cells at the base of the primary erect axis. They likewise branch endogenously, some of the branches remaining prostrate, while others grow erect; erect shoots are also formed from the upturned tips of the creeping axes. The part of the branch within the parent-axis remains monosiphonous and pushes its way between the pericentrals without causing any disorganisation. The endogenous branching of the prostrate shoots contrasts with the exogenous origin of the laterals on the erect ones. Other species (*P. elongata*, *P. violacea*) lack this system of creeping threads and are merely attached by rhizoids emanating from the lower cells of the erect axes; these sometimes combine to form a massive disc (fig. 199 J, *r*).

In *Brongniartella* and some *Polysiphonias* (*P. urceolata*, *P. fastigiata*) the pericentrals remain undivided, but in *P. violacea* for instance, as in many other Rhodomelaceae,[1] they segment by periclinal and anticlinal walls (fig. 206 E) to form a parenchymatous cortex (*co*) of more or less numerous layers ((192) p. 30), whereby the original tier-like structure is obscured. The cells of successive layers generally decrease both in length and width and in the mature thallus the superficial layer may be small-celled (fig. 206 D, E). Such cortex-formation is actually equivalent to the production of branched cell-rows, as is evident from the disposition of the pit-connections. Overlying cortical cells become connected by secondary pits ((558) p. 465).

Cortication by means of septate threads is met with only in few *Polysiphonias*. In *P. Brodiaei* ((192) p. 34, (558) p. 431), where they originate from cells cut off in the lower angles of the pericentrals, they

[1] The process is described in detail by Ambronn ((15) p. 172) for *Halopithys*.

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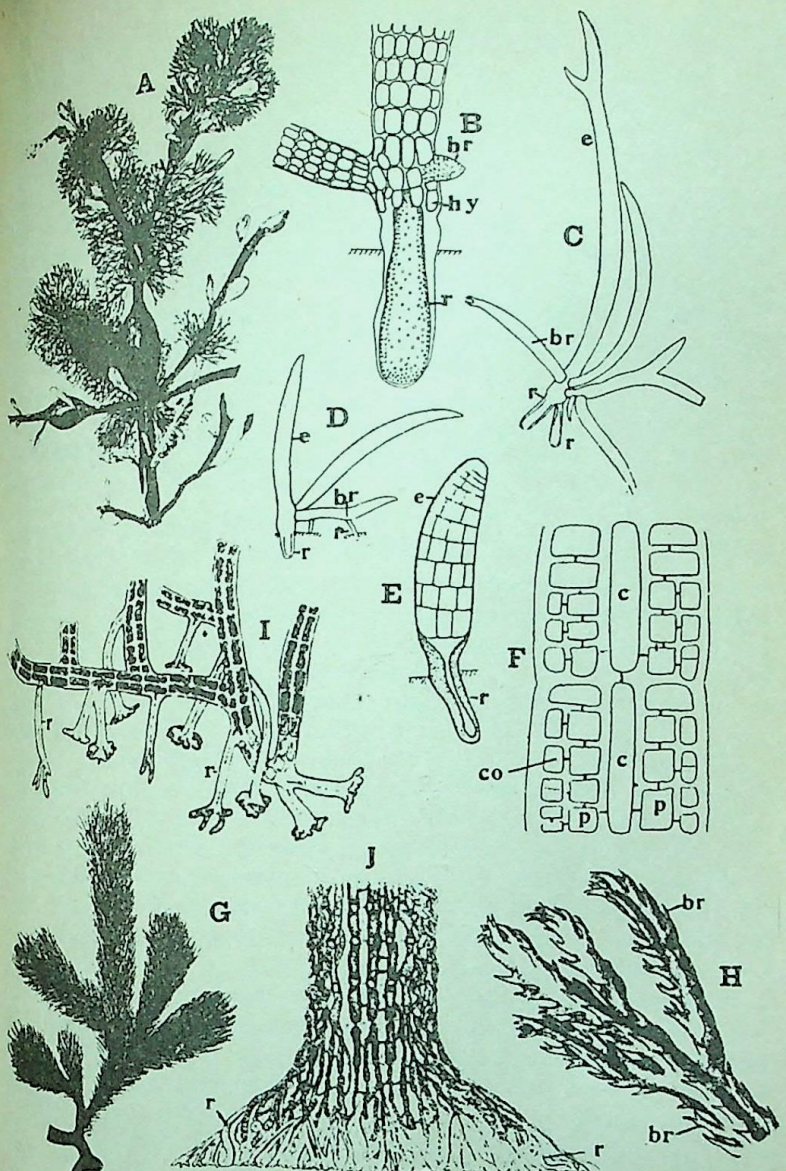

Fig. 199. A–E, *Polysiphonia fastigiata* (Roth) Grev.; A, plants on *Ascophyllum nodosum*; B, lower part of a young plant; C, D, older stages; E, germling. F, *Bostrychia vaga* Hook. & Harv., diagram of longitudinal section through two segments. G, *Digenea simplex* (Wulf.) Ag., habit. H, *Bryothamnion triquetrum* (Gmel.) Howe, part of a plant. I, *Polysiphonia urceolata* Grev., attachment system. J, *P. elongata* (Huds.) Harv., base of plant. *br*, branch; *c*, axial cells; *co*, cortex; *e*, erect axis of germling; *hy*, hyphae; *p*, pericentrals; *r*, rhizoids. (A, I, J after Batten; B–E after Sauvageau; F after Falkenberg; G after Kützing; H after Boergesen.)

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combine to form a thick cortex (fig. 198 N, *co*); here there is also a formation of hyphae (*hy*) between the central and pericentral cells and such are likewise recorded in *P. elongata* ((192) p. 128, (549) p. 3) and *P. violacea* ((54) p. 87, (192) p. 116).

The germlings of *Polysiphonia* ((129) p. 493, (173) p. 251, (379) p. 19, (558) p. 464, (695) p. 11, (699) p. 152) and *Brongniartella* ((115) p. 106, (129) p. 492, (558) p. 449) are of the usual type (fig. 199 E); formation of pericentrals commences early, although a few of the basal cells commonly remain undivided. Older plants are attached by a number of basal rhizoids which unite to form a disc.

Species of *Polysiphonia* are abundant on northern shores, both in the littoral and sublittoral regions. Frequent ecorticate species are *P. urceolata* ((276) pl. 167), with elongate tufts commonly epiphytic on *Laminaria*, and *P. fastigiata* (fig. 199 A; (276) pl. 299), the dark reddish-brown tufts of which are found on *Ascophyllum* (702) and occasionally on *Fucus* ((142) p. 138, (568) p. 214); the former has 4, the latter from 12–24 pericentrals.

The germlings of *P. fastigiata* are usually found within the pits, from which the branches of *Ascophyllum* originate ((25) p. 277, (280), (568) p. 219), and the primary rhizoid (fig. 199 B, E, *r*) penetrates into the medulla without causing any deformation. The pericentrals of the lowest tier produce short hyphae (*hy*) which grow into the thick membrane of the rhizoid and envelop the part external to the host, while at an early stage the central cell gives rise to one or two horizontal runners (fig. 199 B–D, *br*) which develop further rhizoids (*r*) providing for additional anchorage. At these points other erect axes, producing secondary endogenous runners, may originate and, since this may be repeated again and again, *P. fastigiata* spreads over its host like a *Rhizopus*. All the rhizoids become corticated in the same way as the first. *P. fastigiata* is usually spoken of as a parasite but, although some of the host-cells are killed and the fucosan-content is diminished near the rhizoids, there is no evidence of actual absorption of nutriment. Rattray ((533) p. 212) has recorded its occurrence on stones.

P. elongata ((276) pl. 292), a lithophyte reaching a length of 30 cm., is a widely distributed perennial corticate species with 4 pericentrals and abundant trichoblasts. Other frequent corticate forms are *P. Brodiaei* ((276) pl. 195) with 6–8, and *P. nigrescens* (fig. 198 A) with up to 20 pericentrals ((426) p. 108); the former favours rough water. The annual *P. variegata* ((276) pl. 155), with 6 pericentrals, often inhabits polluted water near estuaries, being abundant at Venice ((192) p. 119) and frequent on the roots of Mangroves ((50) p. 269). In *P. spiralis* ((25) p. 287) the 4 pericentrals are spirally twisted (fig. 198 Q) and the same feature is encountered ((558) p. 437) in the dark-coloured *P. nigra* (Huds.) Batt. (*P. atrorubescens* Grev. (276) pl. 172).

Brongniartella byssoides (*Polysiphonia byssoides* (Good. & Wood.) Grev. (276) pl. 284), with 5–7 pericentrals and abundant distichous branching (fig. 198 P), occurs near low-tide level and in deeper water (115).

In a number of southern *Polysiphonias*, all with 4 pericentrals (e.g. *P. hystrix* Hook. et Harv. (270) pl. 14), certain of the laterals are of limited

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growth and alone bear trichoblasts ((192) p. 138). Such dwarf-shoots are also characteristic of *Bryothamnion* ((2) p. 846, (50) p. 282, (192) p. 172, (317) p. 222), the species of which inhabit the warmer Atlantic. Here most of the branches, which are produced on often reduced trichoblasts, appear as short spine-like decurrent structures (fig. 199 H, *br*). The principal axes possess a parenchymatous cortex.

A greater departure from the normal type is seen in *Digenea simplex* ((2) p. 845, (50) pp. 281, 469, (272) p. 30, pl. 13 D), which is widespread in warmer seas (fig. 199 G). A polysiphonous structure is only recognisable in the laterals of limited growth, while the thick cartilaginous axes exhibit a differentiation into medulla and cortex, stated to arise ((192) p. 159, (288)) from the fusion of, and subsequent cell-division in, the basal parts of the laterals.

Falkenbergia ((47) p. 199, (50) p. 331, (54) p. 139, (192) p. 688, (569) p. 19), a genus of doubtful position and possibly only a stage in the life-cycle of *Asparagopsis* (p. 627), is distinguished by the possession of vesicular cells and of only 3 pericentrals, as well as by the origin of the branches (fig. 219 G) from the middle of the youngest pericentral of a segment.

The Lophothalieae, including, apart from *Brongniartella*, the Australian genera *Lophothalia* ((192) p. 534, (592) p. 218) and *Doxodasya* ((192) p. 538), as well as *Murrayella* ((50) p. 314, (192) p. 563, (527) p. 78, (592) p. 227) and the Antarctic *Pteronia* ((192) p. 560, (405) p. 54), resemble *Polysiphonia* in their general radial construction. *Murrayella periclados* (Ag.) Schmitz (*Bostrychia tuomeyi* Harv. (272) p. 58) commonly grows on the roots of mangroves ((48) p. 47). Several members of this tribe show features of special interest in relation to the morphological status of the trichoblasts. The majority of the segments produce unbranched, uniseriate laterals (fig. 200 B, C, *t*), the few cells of which contain chromatophores; some of the basal segments may become polysiphonous. In *Lophothalia* and *Murrayella* the occasional branches replace one of these laterals, but in *Doxodasya bulbochaete* (Harv.) Falkenb.[1] and in *Pteronia* they arise from a basal segment of the latter. *Lophothalia* and *Doxodasya* exhibit cortication (cf. also fig. 200 A), the cortical threads in the latter partly arising from the basal cells of the uniseriate laterals.

Schmitz regarded the uniseriate laterals of these genera as trichoblasts. On the other hand, their tendency to become polysiphonous, the development of identical structures adventitiously in certain species of *Lophothalia* (*L. verticillata*), and the origin of cortical threads from them in *Doxodasya*—respects in which they differ from the trichoblasts of other Rhodomelaceae—led Falkenberg ((192) p. 66) rather to interpret them as arrested branches. Trichoblasts, which are no doubt structures modified for special functions, must be considered to be homologous with the ordinary polysiphonous laterals of

[1] *Dasya bulbochaete* Harv. ((270) pl. 25). Schmitz (592) places *Doxodasya* as a subgenus of *Lophothalia* and, since the only essential difference lies in the method of branching, this is perhaps warranted.

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a *Polysiphonia*, etc. *Lophothalia* and *Doxodasya* would then be generalised types in which the morphological differentiation between the two kinds of laterals is not yet fully established. The persistence of the trichoblasts, and the presence of chromatophores in their cells in many Lophothalieae,[1] warrant our regarding the latter ((192) p. 700) as a primitive group among Rhodomelaceae; Falkenberg derives the Polysiphonieae directly from them by way of *Brongniartella*.

The origin of polysiphonous branches from the trichoblasts in *Brongniartella*, many *Polysiphonias*, and other Rhodomelaceae is probably a secondary condition ((547) p. 15, (549)) which has perhaps been determined by nutritive relations. In view of the homology between the two types of laterals and the tendency to transfer the seat of

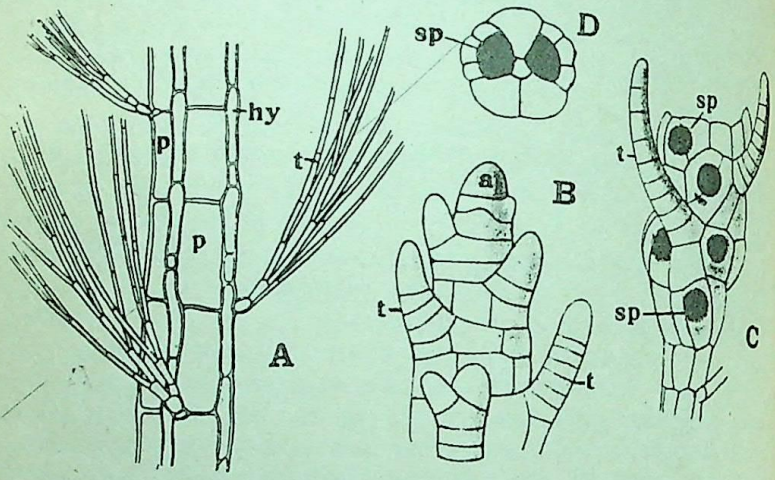

Fig. 200. A, *Lophocladia trichoclados* (C. Ag.) Schmitz, small part of a thread. B–D, *Lophothalia verticillata* (Harv.) Kütz.; B, apex of thallus showing the simple trichoblasts; C, older part with sporangia (*sp*); D, transverse section of a branch with sporangia. *a*, apical cell; *hy*, cortical threads; *p*, pericentrals; *t*, trichoblasts. (A after Boergesen; the rest after Falkenberg.)

development of laterals of unlimited growth to the basal cells of those of limited growth among the less specialised Florideae (cf. e.g. *Batrachospermum*), there is nothing remarkable in this condition. The outgrowth, originating the polysiphonous branch, normally arises from the basal segment of the trichoblast, which only under these circumstances produces a lateral and only then develops a poly-

[1] This is also so in the West Indian *Lophocladia trichoclados* (*Polysiphonia lophoclados* Kütz.; *Dasya lophoclados* Mont. (272) p. 65; *Lophothalia trichoclados* J. Ag.), which is distinguished from other Lophothalieae by the endogenous and adventitious origin of the polysiphonous branches (cf. (50) p. 302, (192) p. 552, (592) p. 222), although in other species some take the place of trichoblasts; cf. also *Wrightiella* (p. 746).

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siphonous structure. The degree of specialisation renders the unravelling of the course of evolution difficult.

Berthold's view ((37) p. 677) that the trichoblasts constitute a protection against intense illumination has not met with much support. Rosenvinge and others ((192) p. 70, (503) p. 390, (557) p. 448) are of the opinion that they aid in the absorption of nutriment and possibly also play a rôle in respiration. Functionally they no doubt replace the unicellular hairs of other Florideae, as to whose rôle the same differences of opinion exist (p. 450). Their frequent restriction to young parts, their common relation to branch-formation, and above all their

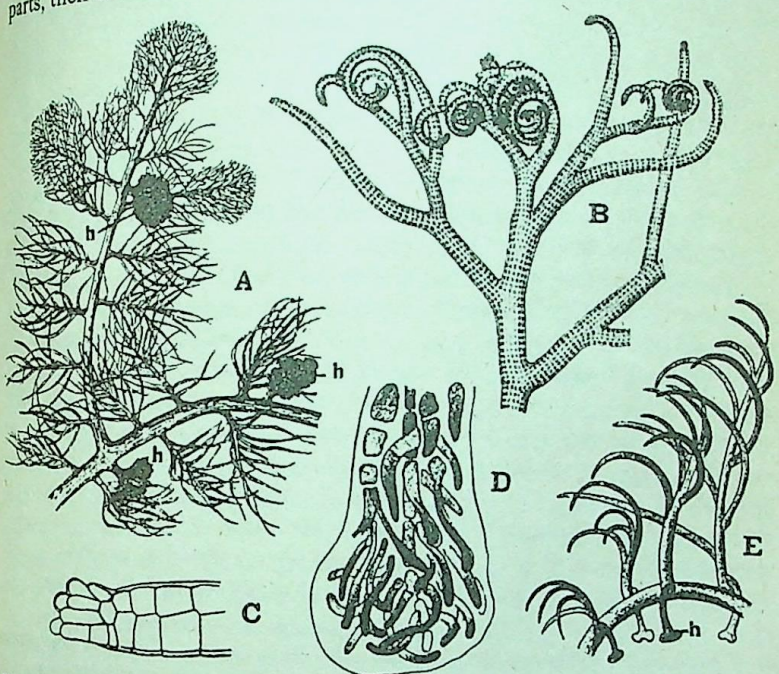

Fig. 201. *Bostrychia*. A, *B. tenella* (Vahl) J. Ag., habit. B, *B. scorpioides* (Gmel.) Mont., apical part of thallus. C, *B. Moritziana* Ag. and D, *B. Hookeri* Harv., tips of branches showing rhizoid development. E, *B. radicans* Mont., part of a plant. *h*, haptera. (A after Boergesen; B after Ambronn; C after Goebel; D, E after Falkenberg.)

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Bostrychieae and Rhodomeleae. Some modification of the *Polysiphonia*-type, combined with a marked dorsiventral tendency, is seen in *Bostrychia* ((2) p. 851, (10) p. 63, (15) p. 193,[1] (50) p. 300, (192) p. 504, (527) p. 4), the species of which favour brackish water. Several (e.g. *B. tenella*, fig. 201 A; *B. Moritziana* Ag.) are characteristic components

[1] As *Helicothamnion scorpioides*. The older name *Amphibia* is not in use, *Bostrychia* being a nomen conservandum.

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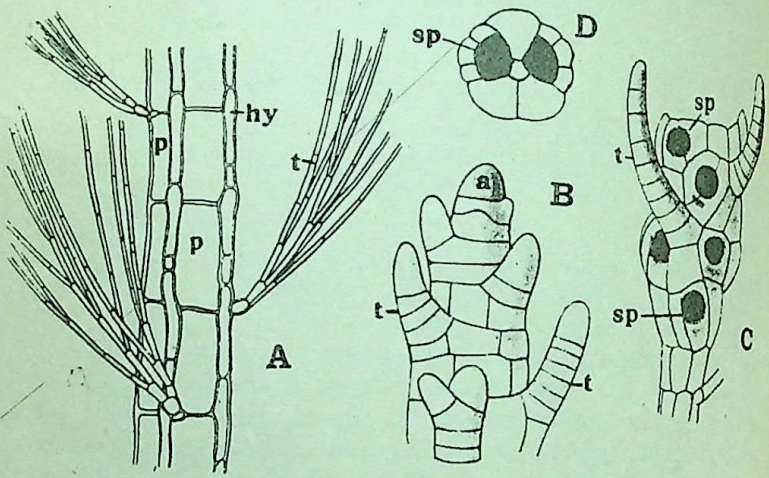

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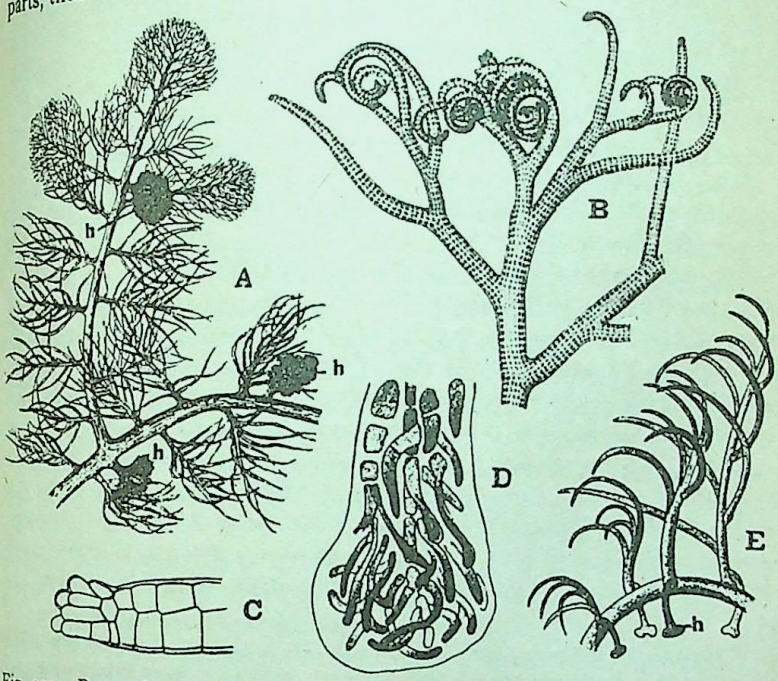

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of the vegetation on the roots of the Mangrove-community in tropical estuaries ((48) p. 45, (684), (687) p. 653, (774)). *B. scorpioides* (fig. 201 B; (276) pl. 48) is frequent in European salt-marshes ((96) pp. 352, 358, (97) p. 207, (101) p. 191, (142) p. 78), while *B. rivularis* Harv.[1] ((272) p. 57) seems to occupy similar habitats in Atlantic North America (cf. (685) p. 375). *B. Moritziana* has been found ((248) p. 437), associated with Podostemaceae, in cataracts of the Amakura (British Guiana) far above the estuarine region.

Part of the thallus is usually prostrate, while the growing apices are commonly curved with the concavity towards the substratum (fig. 201 E), being sometimes (*B. scorpioides*, fig. 201 B) even spirally inrolled. The laterals, many of which are of limited growth, arise in two longitudinal rows, inserted on opposite sides of the axis in the erect *B. calliptera* Mont. and in *B. tenella* (fig. 201 A), but nearer to the dorsal line in most of the prostrate forms (e.g. *B. radicans*, fig. 201 E); the degree of branching varies greatly. Trichoblasts are wanting.

The number of pericentrals is 6–10 in the older parts, but usually dwindles to 4 in the younger (cf. fig. 201 B); in most species the final segments remain undivided. *Bostrychia* and its immediate allies are characterised by the fact that the pericentral cells undergo *horizontal* division, usually into 2 (*B. scorpioides*), but sometimes into 4–6 (e.g. *B. Hookeri*, *B. vaga*, fig. 199 F) cells; the lowest member of the row thus formed retains the pit-connection with the central cell. Subsequently a parenchymatous cortex (*co*) is commonly produced, while cortication by threads is reported in *B. calliptera*. Attachment of the creeping axes is effected by haptera (fig. 201 E, *h*), formed by outgrowth of a group of cortical cells, usually opposite an erect branch. Haptera also commonly develop at the ends of special unbranched laterals (fig. 201 A, *h*; (248) p. 442) which become parenchymatous to the tips (fig. 201 C, D) and bend over towards the substratum. The early stages ((129) p. 495) resemble those of *Polysiphonia*.

Horizontal division of the pericentrals is likewise seen in *Rhodomela* and *Odonthalia* (Rhodomeleae), two widely distributed perennial lithophytes found in the colder seas of the Northern Hemisphere; they also exhibit other signs of specialisation. In *Rhodomela subfusca* (Woodw.) C. Ag.[2] ((276) pl. 264), with a richly branched filiform thallus, each segment of the apical cell produces either a trichoblast or an ordinary branch ((192) p. 593, (371) p. 36, (558) p. 451), the successive laterals lying on a spiral of about 1/4 which usually turns to the left (fig. 202 B), but occasionally to the right ((547) p. 28, (556) p. 360,

[1] Placed as a synonym of *B. radicans* Mont. by Post ((527) p. 13), while the *B. rivularis* of Australia ((277) pl. 176 B) is made the type of a new species, *B. tenuis* (Harv.) Post.

[2] *R. virgata* Kjellm. ((343) p. 110) is regarded by Falkenberg ((192) p. 593) and Rosenvinge ((558) p. 453) as a deep-water form of *R. subfusca*, which is found between tide-levels (cf. however (369) p. 147).

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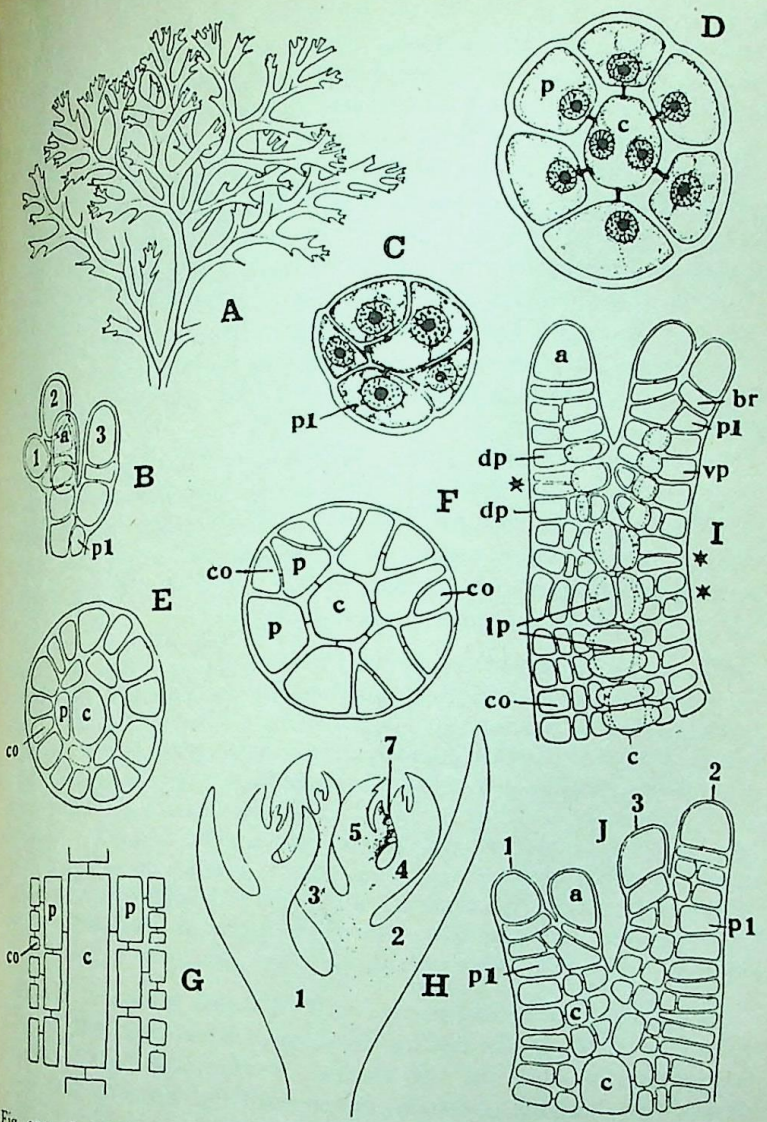

Fig. 202. A, H–J, *Odonthalia dentata* (L.) Lyngb.; A, part of a thallus; H, diagram to show distichous branching (1–7 successive branches); I, apex of a branching thallus, the * marking places where pericentrals have divided horizontally; J, apex showing congenital fusion of laterals (1–3). B–G, *Rhodomela virgata* .Kjellm.; B, apex of a growing shoot (1–3 successive laterals); C, formation of pericentrals; D, pericentral-formation complete, axial cell binucleate; E, F, development of cortex in transverse section; G, in longitudinal section (diagram). *a*, apical cell; *br*, branch; *c*, axial cells; *co*, cortex; *dp*, dorsal pericentrals; *lp*, lateral pericentrals; *p*, pericentrals; *p1*, first-formed pericentral; *vp*, ventral pericentrals. (A after Taylor; H after Falkenberg; the rest after Kylin.)

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(558) p. 455). The ultimate branches bear trichoblasts only. The 6–7 pericentrals develop as in *Polysiphonia* (fig. 202 B, C), but there is no displacement. The trichoblasts, which are shed at an early stage, contain pigmented chromatophores and, unlike those of most Rhodomelaceae, do not bear the sex organs. Adventitious branches are occasionally formed from cells of the cortex.

Each pericentral divides horizontally, the uppermost cell of the row here retaining the pit-connection with the central cell (fig. 202 G), while the lowest becomes linked by secondary connections ((192) p. 596) with the pericentrals of the underlying segment (fig. 147 I, J). The cells of the primary rows cut off (fig. 202 E, F) a number of cortical cells (*co*), each of which again divides horizontally (fig. 202 G, *co*). This process is repeated so that a little way behind the apex there is a 6–7-layered cortex with small peripheral cells, and the polysiphonous structure is obscured.

The radially organised fronds, which arise from a parenchymatous disc, develop mainly in winter and spring. Considerable portions of the plant perish in autumn, only a few of the main axes persisting; from them new shoots arise in the next season ((516) p. 292), in part from arrested rudiments formed in the previous year ((192) p. 594). The young plants are erect ((558) p. 458).

Odonthalia dentata[1] ((192) p. 601, (276) pl. 34, (397) p. 6, (558) p. 459, (742) p. 30, (744) p. 69), distinguished by its flattened, distichously branched fronds (fig. 202 A, H), forms no trichoblasts. Of the 4 pericentrals, the 2 situated on the future flat faces of the fronds (fig. 202 I, *lp*) almost immediately segment longitudinally (rarely transversely, as in the lower part of fig. 202 I), while the other 2 undergo a single horizontal division (see the places marked *). Tangential division, usually more rapid on one side (fig. 202 J), initiates the wings, while the products of the median pericentrals undergo less extensive division to form an, often faint, midrib. The lower parts of the laterals are congenitally fused with their parent-axes (fig. 202 J and p. 560).

Chondrieae and Laurencieae. All outward evidence of a polysiphonous structure is lacking in certain Rhodomelaceae, in which nevertheless a study of the thallus-development behind the apex betrays the essential correspondence with *Polysiphonia*. This is well exemplified by *Chondria* and *Laurencia*. In the rather fleshy thalli of *Chondria*[2] (fig. 203 A, B) the apical cell (fig. 203 D, *a*) is situated at the summit of a narrow cone, which in *C. dasyphylla* is lodged in a deep depression (fig. 203 F); this is lacking in *C. tenuissima*. The segments are cut off by oblique walls along a 3/10 spiral and each forms a trichoblast (*t*); the 5 pericentrals (fig. 203 E) develop in the usual way. In the lower part of the apical cone there is a rapid enlargement

[1] *Rhodomela dentata* Lyngb.
[2] See (192) p. 195, (349) p. 426, (350) p. 98, (387) p. 79, (692) p. 88.

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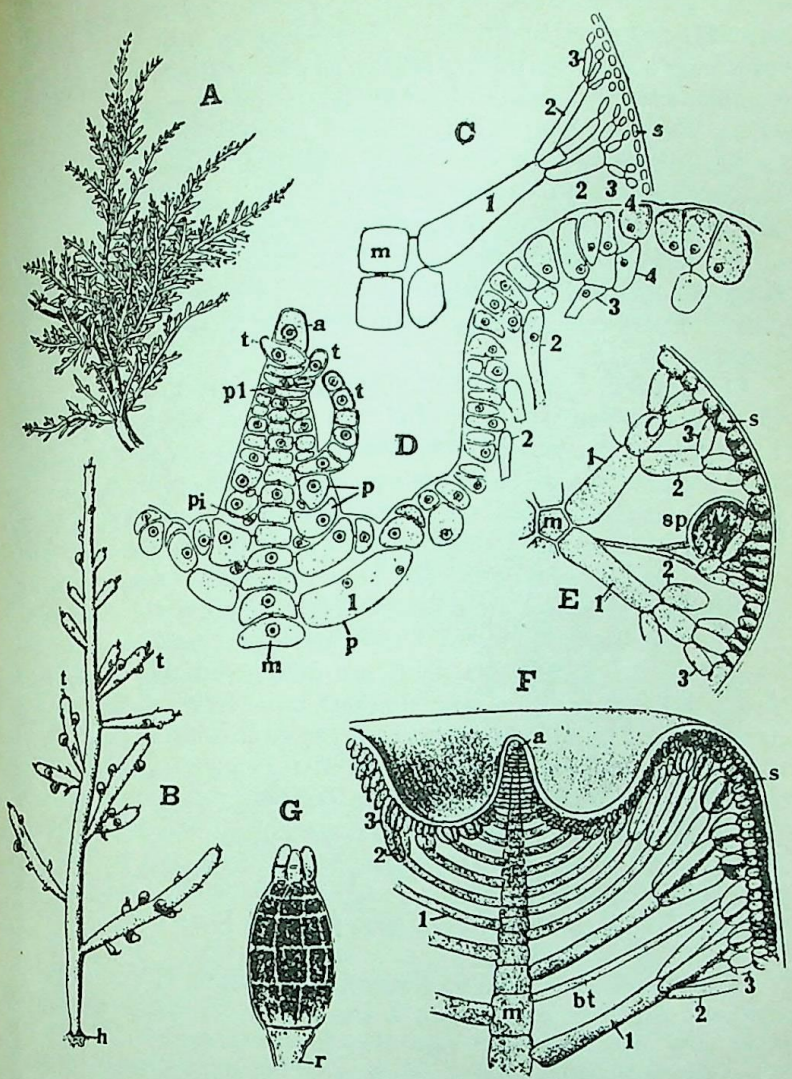

Fig. 203. *Chondria*; E, *C. coerulescens* (Crouan) Falkenb.; G, *C. tenuissima* (Good. & Wood.) C. Ag.; the others *C. dasyphylla* (Woodw.) C. Ag. A, habit; B, young plant; C, small part of a longitudinal section immediately below the apical depression; D, apical cone and part of apical depression in longitudinal section; E, part of a transverse section below the apical depression; F, half of apical part of a branch in longitudinal section; G, germling, only the top of the rhizoid is shown. *1*, *2*, *3*, *4* in C–F, laterals of successive orders; *a*, apical cell; *bt*, basal segment of trichoblast; *h*, attaching organ; *m*, axial cells; *p*, pericentrals; *p1*, first-formed pericentral; *pi*, pit-connection; *r*, rhizoid; *s*, surface-layer of thallus; *sp*, sporangium; *t*, trichoblasts. (A after Taylor; B after Boergesen; C, D after Kylin; E, F after Falkenberg; G after Thuret.)

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of the pericentrals (fig. 203 D, *p*), accompanied by formation of secondary pit-connections (*pi*). At its base the pericentrals undergo branching to the fourth degree (fig. 203 C, *1–4*), while they and their products exhibit marked radial elongation, so that there result alternating whorls of laterals (fig. 203 E, F) which are spatially separated by the enlargement of the central cells (*m*). The final ramifications produce the compact surface-layers (*s*). The apical depression of *C. dasyphylla* results from the great horizontal elongation (fig. 203 D) of the pericentrals (*1*) and of their primary branches (*2*) behind the apex. In the older parts there is marked dilation of the cells which come into lateral contact, with the formation of secondary pit-connections.

The subapical structure of *Chondria* altogether conforms to the *Batrachospermum*-type[1] (cf. fig. 203 E, F), while the progressive branching of the pericentrals clearly corresponds with the mode of production of the parenchymatous cortex in *Polysiphonia*, except for the radial elongation and the spatial separation of the cells (cf. p. 546). *Chondria* and its allies thus serve to demonstrate the close relation between the polysiphonous condition of most Rhodomelaceae and the morphological construction of the primitive uniaxial Nemalionales.

The copiously branched trichoblasts of *Chondria*, which form clusters at the tips (fig. 203 B, *t*), are shed before they are carried out of the apical depression; the elongate basal segment (fig. 203 F, *bt*), however, remains embedded amid the branching pericentrals. The branches of the thallus arise at the distal ends of these segments in essentially the same way as in *Polysiphonia* ((349) p. 427, (387) p. 84). The pericentrals of the second segment of the branch produce hyphae which penetrate into the parent-axis and strengthen the attachment. The early stages ((129) p. 497, (173) p. 249, (692) p. 92) resemble those of other Ceramiales (fig. 203 G).

C. dasyphylla (fig. 203 A; *Laurencia dasyphylla* Grev. (276) pl. 152), common near low-water mark in the North Atlantic, is also recorded from the Mediterranean and the Arabian sea (57). *C. tenuissima* (*Laurencia tenuissima* Grev. ((276) pl. 198) has a greater southward range and is more frequent in warmer seas. Both are annual lithophytes, attached by large holdfasts (fig. 203 B, *h*) formed by numerous rhizoids. *C. crassicaulis* Harv. (491) possesses short branches containing much starch and probably serving as organs of vegetative propagation. *Acanthophora spicifera* ((47) p. 201, (50) p. 259, (727) p. 347; *A. Thierii* Lamour. (272) p. 17; cf. also (192) p. 226), widespread in warmer seas, is characterised by its numerous short spinous branches (fig. 204 E) which arise from the trichoblasts.

[1] This is particularly well seen in the related southern genus *Coeloclonium* ((192) p. 210) where the thalli are markedly inflated (*Chondria opuntioides* Harv. (277) pl. 198, (278) pl. 189).

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The compact thallus of *Laurencia* ((102) p. 238, (380) p. 123, (387) p. 91)[1] is solid throughout (fig. 204 A) and the basic structure is discernible only near the tips. The apex (fig. 204 A) is similar

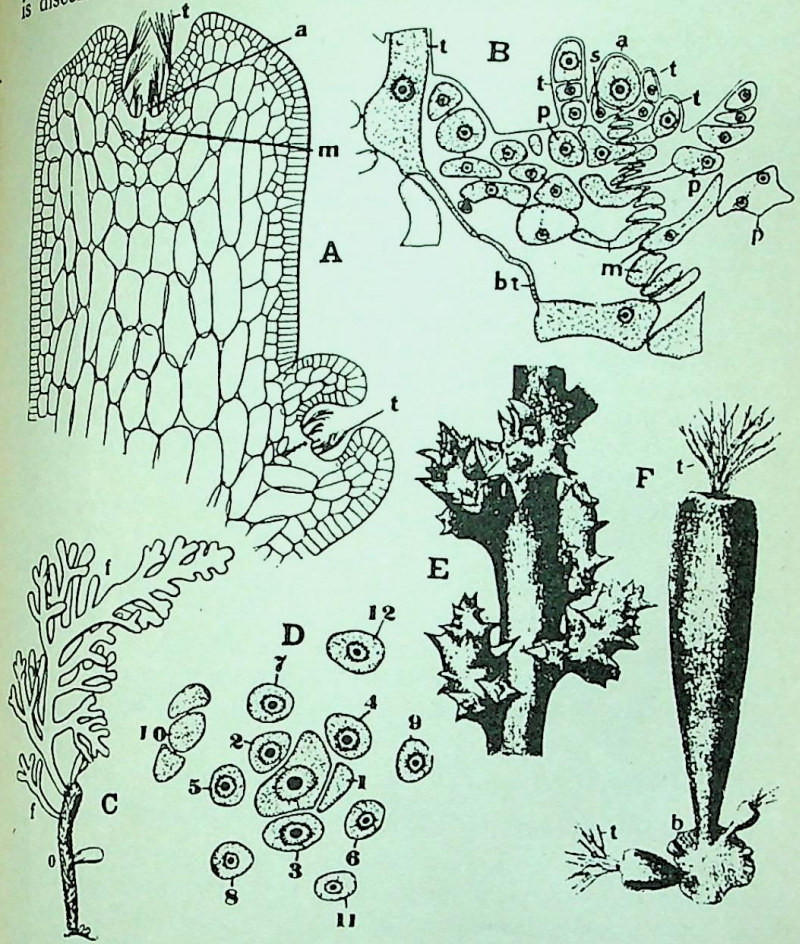

Fig. 204. A–D, F, *Laurencia*; A, *L. obtusa* (Huds.) Lamour.; B, *L. papillosa* (Forsk.) Grev.; C, D, F, *L. pinnatifida* (Gmel.) Lamour. A, longitudinal section of tip of thallus, with a lateral; B, apical cone in longitudinal section; C, new fronds (*f*) arising from last season's growth (*o*); D, transverse section through apex showing disposition of trichoblasts (*1–12*); F, young plant. E, *Acanthophora spicifera* (Vahl) Boerges., small part of a shoot. *a*, apical cell; *b*, basal disc; *bt*, basal segment of trichoblast; *m*, axial cells; *p*, pericentrals; *s*, segment; *t*, trichoblasts. (A after Falkenberg; B, D after Kylin; C, F after Rosenvinge; E after Boergesen.)

to that of *Chondria*, but the apical cell (fig. 204 B, *a*) produces three rows of segments. All of these form richly branched deciduous

[1] Naegeli's account ((475) p. 220) is partly erroneous. The taxonomy of the genus is dealt with by Yamada (752).

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trichoblasts which are arranged spirally (fig. 204 D, *1–12*). The branches arise from the trichoblasts, in *L. pinnatifida* only from those situated on the flanks so that the branching is distichous (fig. 204 C). The bases of the older branches become embedded in the peripheral tissue of the axis.

The wedge-shaped segments (fig. 204 B, *s*) of the apical cell (*a*) cut off on either side, beneath the trichoblast (*t*), 2 pericentrals (*p*; 3 according to (192) p. 239) and no more are produced (cf. *Cystoclonium*, etc.). The cortex is formed in much the same way as in *Chondria*, but the central cells (*m*), which become transversely extended, are clearly distinguishable only near the apex (fig. 204 A, *m*) and there is no appreciable extension of the outer cells. During the abundant cell-division at the base of the apical depression the basal segments of the trichoblasts become drawn out into long and narrow threads (fig. 204 B, *bt*). The mature parts display little differentiation (fig. 204 A). The early development follows the usual course ((129) p. 498, (379) p. 20).

L. pinnatifida ((276) pl. 55), a lithophyte frequently found in the lower part of the intertidal region, has pinnately branched cartilaginous thalli (fig. 204 C), with the larger branches often flattened. The fleshy and parenchymatous attaching disc is full of starch and produces a number of erect shoots (fig. 204 F), the basal parts of which commonly last for several seasons ((353) p. 52, (558) p. 404), the new season's growth being often readily distinguishable from the old (fig. 204 C). A similar condition is reported in other species ((662) p. 212). In *L. obtusa*, an epiphyte with cylindrical thalli, more frequent in warmer seas, the branches of higher orders tend to appear whorled owing to the restriction of branch-formation to occasional groups of trichoblasts ((50) p. 247, (192) p. 247).

(ii) *Rhodomelaceae with Bilateral and Dorsiventral Construction*

A considerable number of Rhodomelaceae, while retaining the tier-like structure of a *Polysiphonia*, exhibit specialisation in the acquisition of bilateral or dorsiventral symmetry. Examples of this trend have already been seen in the bilateral habit of *Odonthalia* (p. 554) and the dorsiventral construction of many *Bostrychias* (p. 552), but these genera are closely allied to radially organised types. Among the Pterosiphonieae and Herposiphonieae, however, these tendencies become paramount and, combined with other special developments, culminate in a number of exceptional types. Neither light nor gravity appear to play a rôle in determining dorsiventrality within this family ((192) p. 81).

Pterosiphonieae and Herposiphonieae. The species of *Pterosiphonia* ((192) p. 261) are small forms favouring the warmer seas. The principal axes are prostrate (fig. 207 A, *pr*) and attached by rhizoids (*r*), but their younger parts become erect and show distichous branching, combined with a tendency to flattening so that a pinnate habit results. There are no trichoblasts. The branches (fig. 207 A; B, *1*, *2*) arise from alternate

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segments on the erect shoots, at wider intervals on the creeping ones; these latter branches may at first be prostrate. Most species are devoid of a cortex.

The branch-forming segments (fig. 207 B, *se*) are markedly oblique, and the septum cutting off the initial (*l*) arises before there is any

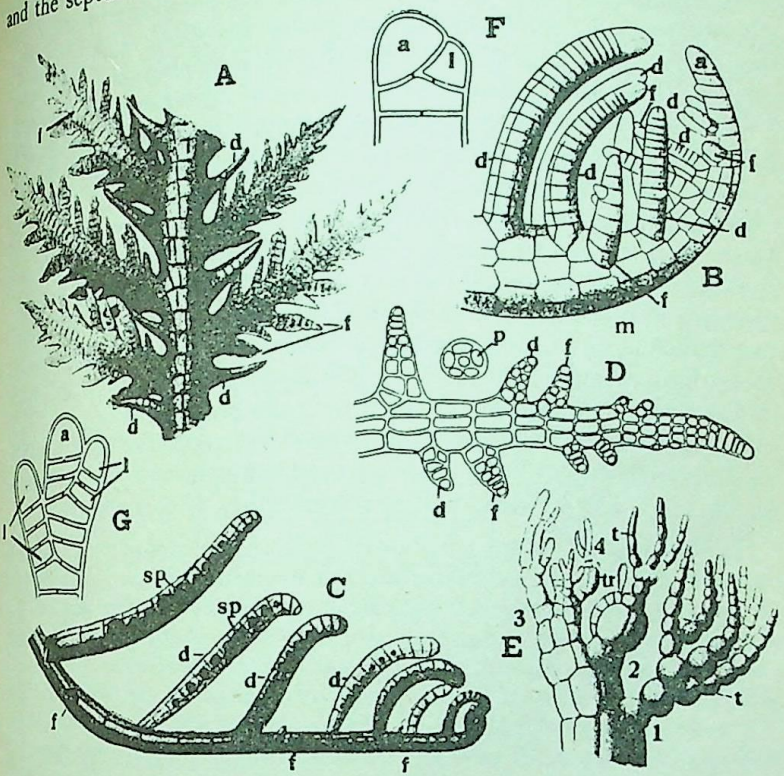

Fig. 205. A, *Dipterosiphonia heteroclada* (J. Ag.) Falkenb., habit. B, *Herposiphonia tenella* (C. Ag.) Falkenb., apex of thallus. C, E, *H. secunda* (C. Ag.) Falkenb.; C, apex of thallus; E, apex of shoot of limited growth, with trichoblasts (*t*) and procarp (*tr*). D, *Dipterosiphonia dendritica* (Ag.) Falkenb., view of apex of thallus to show branching; above, transverse section. F, G, diagrams showing branching, accompanied by congenital fusion. *a*, apical cell; *d*, dorsal branches of limited growth; *f*, branches arising on the flanks; *l*, laterals; *m*, main axis; *p*, pericentral; *sp*, sporangia; *tr*, trichogyne. (D after Boergesen; the rest after Falkenberg.)

marked protrusion and in such a way that a considerable area of wall is common to the initial and the apical cell (fig. 205 F, *l*). The first septa in the initial abut on this common wall (fig. 205 G, *l*) and, as a result, a number of the basal segments of the branches are congenitally fused with the parent-axis (see * in fig. 207 B); in the region of fusion the lateral develops pericentrals only on the abaxial side ((1092) p. 58). The congenital fusion is more marked in *P. complanata*

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Schmitz (*Rytiphloea complanata* Harv. (276) pl. 170) than in *P. parasitica* (*Polysiphonia parasitica* Grev. (276) pl. 147) and, as in *Odonthalia* (cf. fig. 202 J), is in part responsible for the flattening of the fronds. The germlings ((129) p. 495) are like those of *Polysiphonia*.

The dorsiventral organisation of the Herposiphonieae is exemplified by *Herposiphonia*, the species of which are small epiphytes of the warmer seas. In *H. tenella* (*Polysiphonia tenella* J. Ag.; (15) p. 197, (50) p. 286, (192) p. 304, (245) p. 359, (474[1])) the long axes are prostrate and attached by unicellular rhizoids, the apex in growing plants being coiled, with the convexity towards the substratum (fig. 205 B). The branches, one generally produced from each segment,[1] arise in strict acropetal succession and stand in four rows (fig. 205 B, C). The two occupying the flanks (*f*) develop into prostrate long shoots, while those situated on the dorsal side (*d*) give rise to erect unbranched laterals of limited growth; as a general rule three successive dwarf-shoots are followed by a long shoot situated on the same side as the last dwarf-shoot of the preceding segment (fig. 206 A), but occasional irregularities occur. The few trichoblasts are restricted to the apices of the dorsal laterals and as usual bear the sex organs (fig. 205 E, *t*). According to Goebel ((245) p. 361) vegetative reproduction takes place by the dying away of the older parts of the principal axes. Berthold ((37) p. 581) has studied the light-orientation of this species.

Dipterosiphonia ((50) p. 292, (192) p. 320), the species of which occur in warmer seas (several in Australasia), is essentially similar, but the prostrate and often flattened fronds have straight apices (fig. 205 D). The laterals, which arise in pairs on alternate sides of the parent-axis (figs. 205 D; 206 B), are entirely prostrate in *D. dendritica* (fig. 205 D; *Polysiphonia dendritica* C. Ag.) and other species. In the Australian *D. heteroclada* (*Polysiphonia dendritica* Harv. (274) p. 232) the dorsal laterals (fig. 205 A, *d*) take the form of more or less curved spines.

The congenital fusion seen in *Pterosiphonia* is more pronounced in other Pterosiphonieae and in certain Herposiphonieae. A good example is furnished by *Symphyocladia marchantioides*[2] ((192) p. 276), known only from New Zealand, in which the flat prostrate thallus (fig. 207 C) is composed of two layers of pericentrals (fig. 206 F, *p*) with an intervening row of central cells (*c*); the latter appear as veins traversing the thallus. The one-layered margin (fig. 207 E) is occupied by a row of initials and their segments. The former (*1–5*) belong to successive laterals, produced alternately to right and left from every second segment and congenitally fused throughout their length with their parent axis (cf. also fig. 206 C); the arrangement of the laterals is clear from the disposition of the branch veins. The lobes of the thallus are formed by outgrowth of laterals of the second order. The

[1] Naegeli's account is erroneous in certain respects. In *H. secunda* only some of the segments bear branches (fig. 205 C).

[2] *Amansia ? marchantioides* Harv. ((274) p. 223).

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individual axes occasionally become free towards the end of their growth, their apical cells still cutting off a few segments, each of which produces a trichoblast.

The Australian *Pollexfenia pedicellata* ((190), (192) p. 290, (270) pl. 5) has a similar habit (fig. 207 G). The growing margin (fig. 207 H)

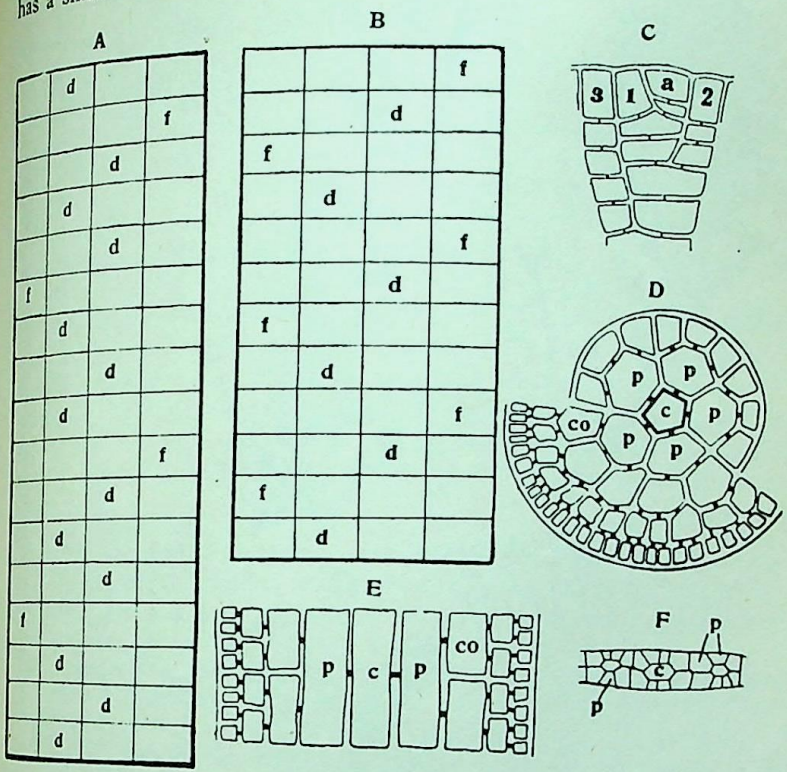

Fig. 206. A, scheme of branching of *Herposiphonia*. B, the same of *Dipterosiphonia*. C, F, *Symphyocladia marchantioides* (Harv.) Falkenb.; C, diagram illustrating branching and congenital fusion, *1–3* successive branches; F, transverse section of thallus. D, E, diagrams of cortex-formation in Rhodomelaceae; D, transverse; E, longitudinal. *a*, apical cell; *c*, central cell; *co*, cortex; *d*, dorsal laterals; *f*, laterals situated on the flanks; *p*, pericentrals. (All after Falkenberg.)

resembles that of *Symphyocladia*, although each segment produces a branch; there is the same congenital fusion. The veins of the thallus, again constituted by the central cells, show clearly the sequence of branching (fig. 207 F). *Pollexfenia* has 4, *Symphyocladia* 6–8 pericentrals. Another variant on this type of construction is afforded by the handsome *Dictymenia* (cf. p. 746 and fig. 299 B).

In *Pollexfenia* the laterals are arranged in four rows. Two, which are situated on the flanks (fig. 207 H, *1–8*), develop vigorously and join to

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form the flat thallus, while those arising on the dorsal and ventral surfaces (*s*, *s'* in fig. 207 F, H), which are not included in the congenital

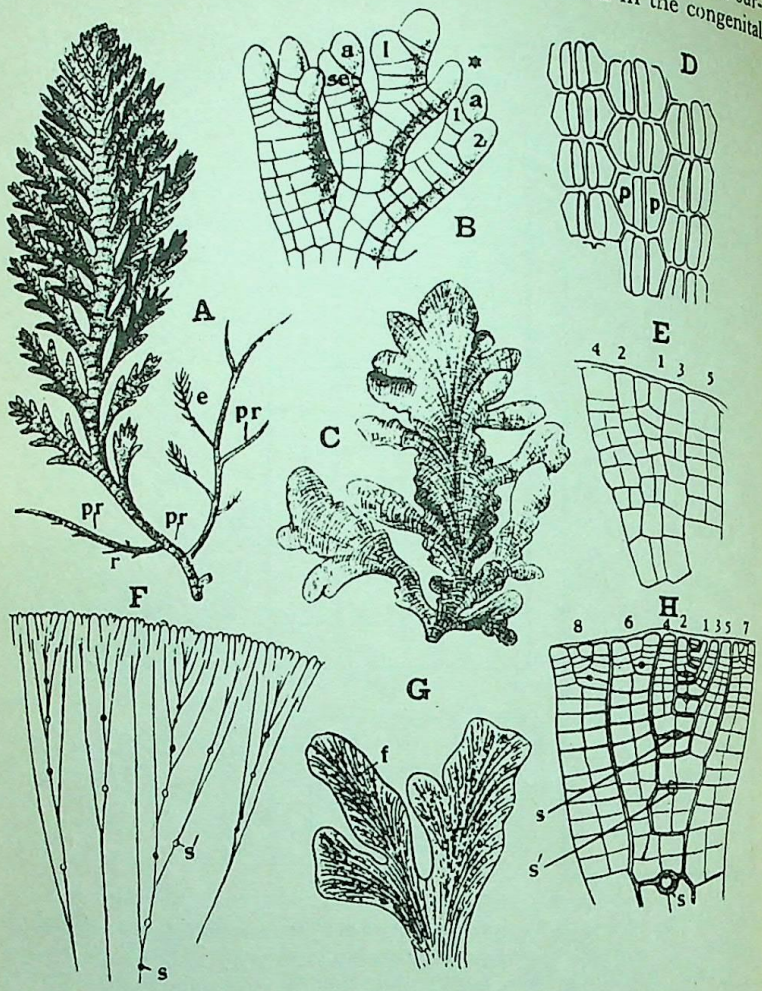

Fig. 207. A, B, *Pterosiphonia parasitica* (Huds.) Falkenb.; A, habit; B, apical part of an erect shoot. C–E, *Symphyocladia marchantioides* (Harv.) Falkenb.; C, habit; D, surface-view of part of thallus, with fully developed pericentrals; E, edge of thallus from the surface. F, G, H, *Pollexfenia pedicellata* Harv.; F, diagram of thallus to illustrate mode of branching; G, habit, showing the fertile laterals (*f*); H, edge of thallus from the surface. *1*, *2*, *3*, *4*, *5*, etc. in E and H, apical cells of successive congenitally fused laterals; *a*, apical cell; *e*, erect frond; *l*, lateral; *p*, pericentral; *pr*, prostrate branches; *r*, rhizoid; *s*, *s'* (in F and H), points of attachment of laterals standing perpendicular to general plane of branching; *se*, segment. (After Falkenberg.)

fusion and may remain arrested for a time, appear as short polysiphonous branches of the usual type; they produce a richly branched trichoblast from each segment and bear the reproductive organs. In

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P. crispata (Zanard.) Falkenb.[1] ((192) p. 296) the dorsal and ventral laterals are recognisable only near the growing margin, and the reproductive organs are borne on the free tips of the elsewhere fused branches. The prostrate part of the thallus of *P. pedicellata* is attached by massive haptera formed from the ventral pericentrals.

While *Symphyocladia* and *Pollexfenia* to all intents and purposes exhibit the bilateral symmetry of the simpler Pterosiphonieae, *Placophora* ((2) p. 1137, (6) p. 111, (190) p. 164, (192) p. 336, (247) p. 3), a parallel form among Herposiphonieae, shows a dorsiventral organisation. The thallus of *P. Binderi* (fig. 208 A), an epiphyte on *Codium* reported from South Africa and Peru,[2] agrees in its marginal growth and congenital fusion (fig. 208 B) with the corresponding forms among Herposiphonieae. Each segment produces a branch, and the laterals arise in pairs (*1*, *1*, *2*, *2*, etc.), alternately to the right and left (cf. *Dipterosiphonia*). The primary laterals first divide by walls parallel to the margin and the resulting segments (*s*) produce no branches, which as usual are formed as a result of later oblique septation. Occasional branches may sometimes project above the surface. The segments form 5 pericentrals (fig. 208 E), 2 on the ventral (*vp*) and 3 on the dorsal surface (*dp*), some of the former growing out into elongate rhizoids.

Amplisiphonia (308), a Californian lithophyte, has the same vegetative structure, though the thallus is appreciably larger, while the epiphytic *Periphykon* (728) has 4 dorsal and 2 ventral pericentrals, the former undergoing transverse division.

The reproductive organs of *Placophora* are formed on tufts of free branches (cf. *Pollexfenia crispata*) which appear between the lobes of the thallus (fig. 208 A, *r*); those bearing sporangia (fig. 208 F) may consist of 30–50 segments with 8–9 pericentrals, while the sex organs arise on trichoblasts borne in a single dorsal row on the fertile branches. In *Amplisiphonia* tetrasporangia are formed in modified erect-growing marginal lobes of the thallus which possess 6 pericentrals.

The germlings of *Pollexfenia* ((192) p. 290) and *Placophora*[3] possess an erect, radially organised, polysiphonous axis (fig. 208 C, *e*), from the basal segments of which the flat thalli (*m*) arise; in *Placophora* their origin is endogenous. The primary axis of 30–45 segments bears as its only branches a few apical trichoblasts. It can hardly be doubted that in *Pterosiphonia*, *Symphyocladia*, and other prostrate forms among Rhodomelaceae a similar origin of the prostrate shoots will be established. Despite the extreme modification which many of the genera

[1] *Melanoseris crispata* Zanard. ((764) p. 489).

[2] Probably more widely distributed in the Southern Hemisphere (see (727) p. 364).

[3] These stages were described by Askenasy (20) under the name of *Rhodopeltis Geyleri*.

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just considered exhibit, their early development shows that they are derivatives of erect-growing radially organised *Polysiphonia*-like types. It may not be amiss to emphasise that *Symphyocladia* is essentially a

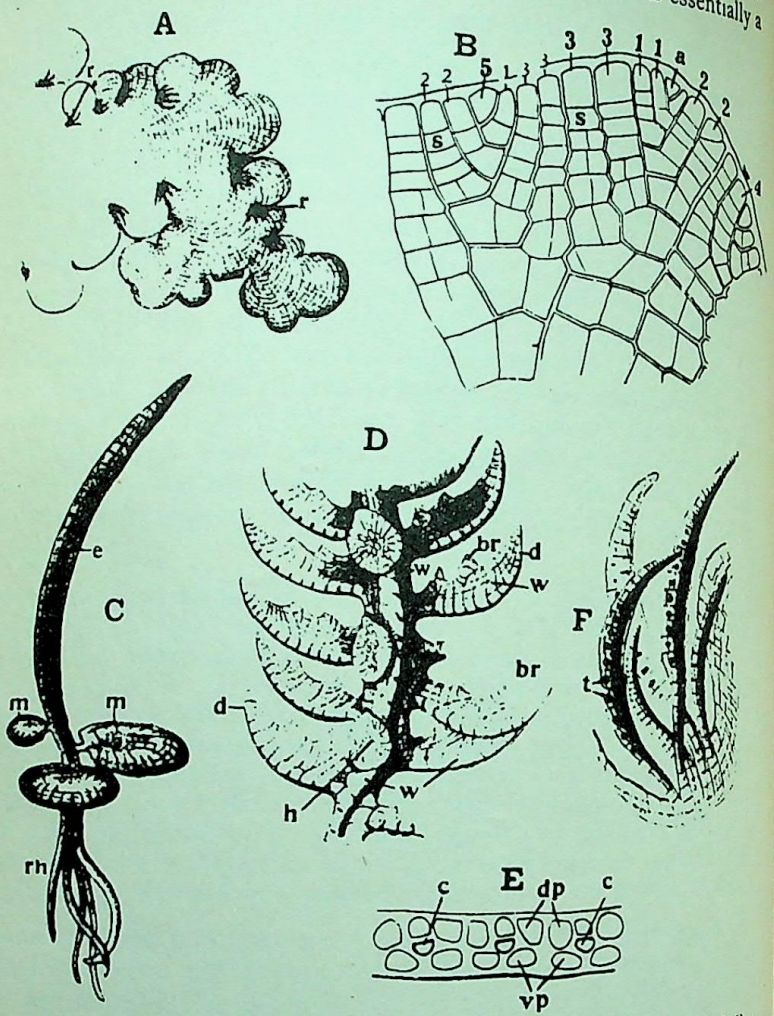

Fig. 208. A–C, E, F, *Placophora Binderi* J. Ag.; A, habit; B, edge of thallus in surface-view, *1*, *2*, *3*, etc. the paired congenitally fused laterals; C, young stage; E, transverse section of flat thallus; F, a group of sporangium-bearing branches. D, *Polyzonia elegans* Suhr, habit (view from ventral surface). *a*, apical cell; *br*, branch; *c*, central cells; *d*, exogenous laterals of limited growth; *dp*, dorsal pericentrals; *e*, erect axis of germling; *h*, hapteron; *m*, mature thalli arising from latter; *r*, reproductive branches; *rh*, rhizoids; *s*, segment; *t*, tetrasporangium; *vp*, ventral pericentrals; *w*, wing. (After Falkenberg.)

Pterosiphonia, *Placophora* a *Dipterosiphonia*, modified by the extreme congenital fusion of the bilateral branch-systems.

Polyzonieae. Considerable morphological specialisation, combined

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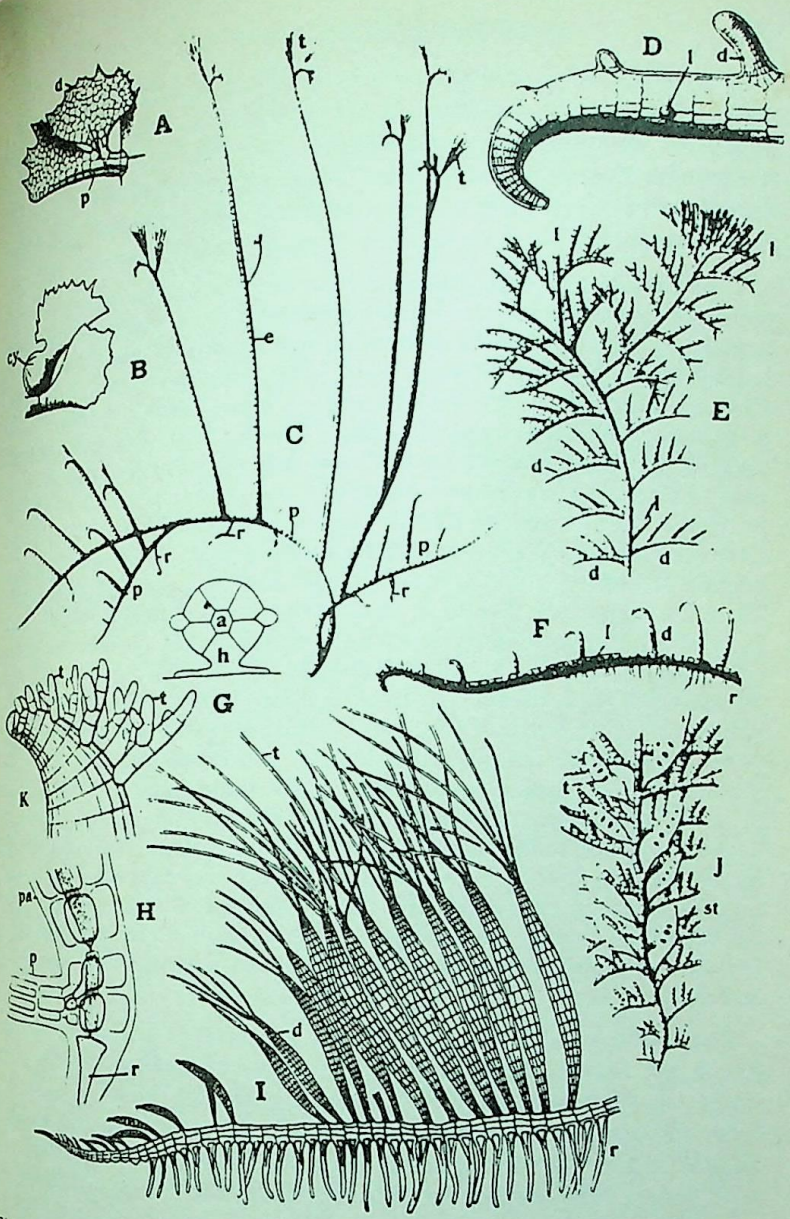

Fig. 209. A, B, *Euzoniella adiantiformis* (Decsne) Falkenb., small parts o plants with two laterals of limited growth, in B one with a cystocarp C, *Lophosiphonia cristata* Falkenb., habit. D, F, *Ophidocladus simpliciuscul* (Crouan) Falkenb.; D, apex of thallus; F, habit. E, G, H, J, *Euzoniell incisa* (J. Ag.) Falkenb.; E, view of part of a sterile plant from above; G, trans verse section of axis, diagrammatic; H, basal part of germling; J, part o branch-system, with sporangial laterals (stichidia). I, *Stictothamnion cymato philum* Boerges., habit. K, *Ctenosiphonia hypnoides* (Welw.) Falkenb., apex of a lateral of limited growth. *a*, axial cell; *cy*, cystocarp; *d*, dorsal shoots o limited growth; *e*, erect shoot; *h*, hapteron; *l*, laterals of limited growth *p*, prostrate shoots; *pa*, primary axis; *r*, rhizoids; *st*, stichidium; *t*, tricho blasts. (I after Boergesen; the rest after Falkenberg.)

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with dorsiventral organisation, is attained in a different way among the Polyzonieae ((192) p. 359), most of which are inhabitants of the Southern Hemisphere, while several are peculiar to Australasia. A common feature is the endogenous origin of the branches of unlimited growth. Several of the extreme forms show resemblance to leafy liverworts.

There are several creeping dorsiventral Rhodomelaceae which show points of contact with the Herposiphonieae, but resemble the Polyzonieae in their endogenous branching. Examples are furnished by *Lophosiphonia* (fig. 209 C; (50) p. 294, (140) p. 126, (192) p. 495, (727) p. 367), *Ctenosiphonia* ((68) p. 67, (192) p. 485), *Ophidocladus* (fig. 209 F; (192) p. 488), and *Stictothamnion* (fig. 209 I; (54) p. 118). Most of these are inhabitants of the warmer parts of the Atlantic; *Lophosiphonia obscura* (Ag.) Falkenb. (*Polysiphonia obscura* J. Ag. (276) pl. 102 A) is known from the south coast of Britain and *Ctenosiphonia hypnoides* (*Polysiphonia hypnoides* Welw.) is reported from Guernsey ((436) p. 20). The laterals of limited growth, for the most part unbranched, grow erect. They are sometimes borne in two rows on the flanks (*Ctenosiphonia*, fig. 209 K), but commonly in a single dorsal row (*Ophidocladus simpliciuscula*,[1] fig. 209 D, F; *Stictothamnion*, fig. 209 I); those of *Stictothamnion* (*d*) are fusiform. In *Lophosiphonia* long and dwarf shoots are not sharply differentiated (fig. 209 C) and some of them (*p*) bend down to the substratum. In *Ophidocladus* (fig. 209 D, F) shoots of unlimited growth (*l*) arise from opposite flanks of the same segment, although one or other often remains arrested. Trichoblasts (fig. 209 C, I, *t*) are usually confined to the tips of the erect laterals, those of *Stictothamnion* being unbranched. In *Falkenbergiella* ((401) p. 21) they are formed only on sexual plants. Although the exact affinities of these genera, which for convenience may be grouped as Lophosiphonieae, are difficult to assess, they help to emphasise the relationship between Herposiphonieae and Polyzonieae.

Euzoniella ((141) p. 150, (192) pp. 73, 360, (408) p. 514) and *Polyzonia* ((14) p. 75, (192) p. 388) comprise a number of small epiphytes of the Southern Hemisphere. Their creeping thallus arises exogenously from the erect primary axis (fig. 209 H, *pa*) which, in *Polyzonia*, is winged as a result of tangential division of opposite pericentrals. In both genera the prostrate laterals arise from the flanks of the creeping axes (figs. 208 D; 209 E), those of limited growth (*d*) exogenously from every second segment, the later-formed long shoots (*l*) endogenously (cf. (14)) from certain intervening segments. The disposition of the two kinds of laterals is much as in *Dipterosiphonia* (cf. especially *Euzoniella incisa*,[2] fig. 209 E). In *Polyzonia* (fig. 208 D) the long axes develop a ventral keel (*w*).

The laterals of limited growth bear short branches on the dorsal side, and in *Euzoniella adiantiformis* these are congenitally fused to

[1] *Polysiphonia simpliciuscula* Crouan ((149) p. 157).
[2] *Polyzonia incisa* J. Ag.; *P. Sonderi* Harv. ((277) pl. 42 A).

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form leafy expanses (fig. 209 A, B). In *Polyzonia elegans* (fig. 208 D, (277) pl. 28), on the other hand, the foliose form of the dwarf-shoots (*d*) is due to the production of one-layered wings (*w*) by tangential division of the single ventral and of one of the two dorsal pericentrals; the branches (*br*) appear as teeth along the margin. This epiphyte is attached by massive haptera (*h*), like those of *Leveillea* (cf. p. 568).

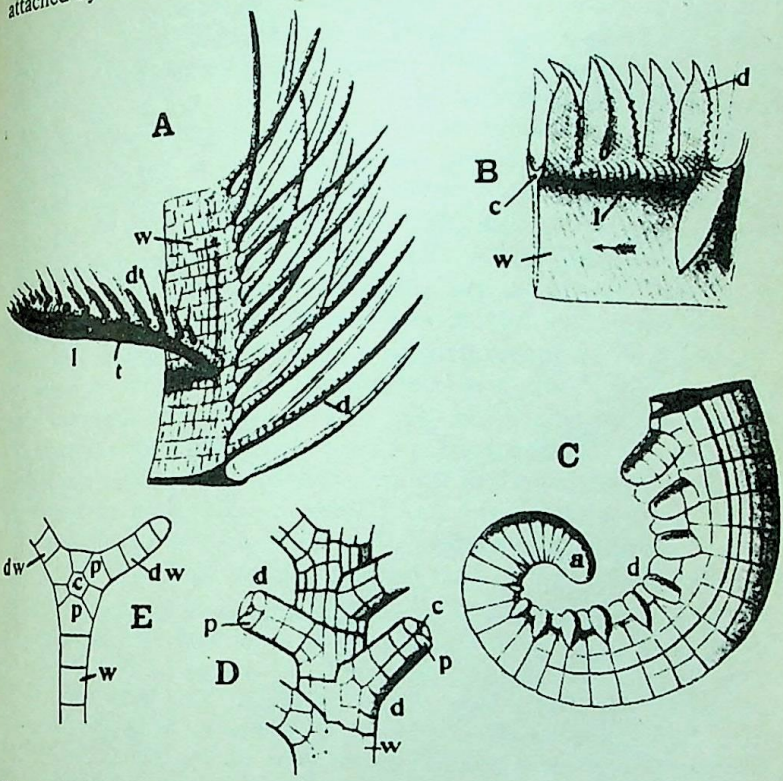

Fig. 210. *Cliftonaea*; A, C, D, *C. pectinata* Harv.; B, E, *C. Lamourouxii* Harv. A, part of a plant, bearing a long lateral (*l*); B, ditto, the arrow pointing towards the apex; C, apex of a long shoot; D, view of part of a long shoot from the upper surface, the short shoots cut off a little way above their base; E, transverse section of a long shoot. *a*, apical cell; *c*, central cell; *d*, branches of limited growth; *dw*, dorsal wings; *l*, branch of unlimited growth; *p*, pericentrals; *t*, tetrasporangia; *w*, wings. (After Falkenberg.)

The ventral wing seen in *Polyzonia* is more markedly developed (fig. 210 A, E, *w*) in *Cliftonaea* ((6) p. 113, (192) p. 373), where the principal axes mostly grow erect and possess strongly inrolled apices (fig. 210 C). The laterals of limited growth (fig. 210 A, C, *d*) form two dorsal rows and, like those of *Polyzonia*, possess only 3 pericentrals (fig. 210 D, *p*), whereas the long branches with 6 pericentrals (fig. 210 E, *p*) arise on the flanks (fig. 210 A, *l*). The ventral wing (fig. 210 E, *w*) is produced by tangential division of the median pericentral, while

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less strongly developed dorsal wings (*dw*), formed from the dorso-lateral pericentrals, link up the bases of the laterals of limited growth. In *C. pectinata* (fig. 210 A; (277) pl. 100) these wings are less pronounced than in *C. Lamourouxii* Harv. ((277) pl. 279), where the ventral pericentral of the short laterals likewise forms a wing (cf. *Polyzonia elegans*). In this species these laterals bear a row of dorsal trichoblasts, whilst in *C. pectinata* they are confined to the sexual shoots. *Polyzonia* and *Cliftonaea*, though presenting points of analogy with *Dipterosiphonia*, exhibit pronounced dorsiventrality in the development of the ventral wing.

The most remarkable member of the Polyzonieae is *Leveillea jungermannioides* ((14) p. 76, (192) p. 392, (245) p. 363, (277) pl. 171), widely distributed in the Indian Ocean and recorded also from the Persian Gulf and Arabian Sea ((57), (62) p. 132). Here the laterals of limited growth (fig. 211 A, *l*), arising from the creeping axes (*cr*), take the form of delicate "leaves", which are attached by a broad base and overlap one another by their posterior edges so that there is a marked resemblance to a Jungermanniaceous liverwort. The creeping shoots (fig. 211 D, *cr*) again arise exogenously from the erect primary axis (*pa*), which is winged like that of *Polyzonia*. The branches of the creeping axis (fig. 211 A, *u*) arise in pairs from the basal segments of two consecutive laterals of limited growth,[1] so that each later appears in the angle between the parent-axis and the front margin of the "leaf"; many remain undeveloped. They possess 7 pericentrals (fig. 211 B), the two ventral ones forming a slight keel.

The short laterals arise as cylindrical outgrowths (fig. 211 C, *l*) within the inrolled apices of the long shoots, as usual from alternate segments. They have 3 pericentrals (fig. 211 I, *p*), the dorsal first-formed one occupying the abaxial side of the rudiment. The foliar form results from active division of the ventral pericentrals, while the broad and oblique attachment is attained by division of the cells of the adjacent segments of the axis, although no continuous wing is formed. Occasionally the apices of these laterals remain cylindrical and produce a double row of dorsal trichoblasts. Attachment is effected by massive haptera (fig. 211 A, D, *h*), formed by the outgrowth of small cells cut off from the ventral pericentral (fig. 211 B, *h*) of two consecutive segments.

Amansieae. A different type of dorsiventral development, often combined with wing-formation in the plane of branching, is seen in the Amansieae ((192) p. 402). The fronds here grow erect, which shows that dorsiventral organisation in Rhodomelaceae is not definitely linked with a creeping habit (cf. also *Cliftonaea*). The fronds usually arise in tufts from a common basal disc. The early development is not known for any representative of this group, but an erect polysiphonous primary axis is to be suspected. Several genera of Aman-

[1] Ambronn and Goebel do not describe these features correctly.

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sieae are confined to the Southern Hemisphere and there are a number of characteristic Australian forms.

Halopithys pinastroides[1] (fig. 211 F; (15) p. 163, (189), (192) p. 472) and

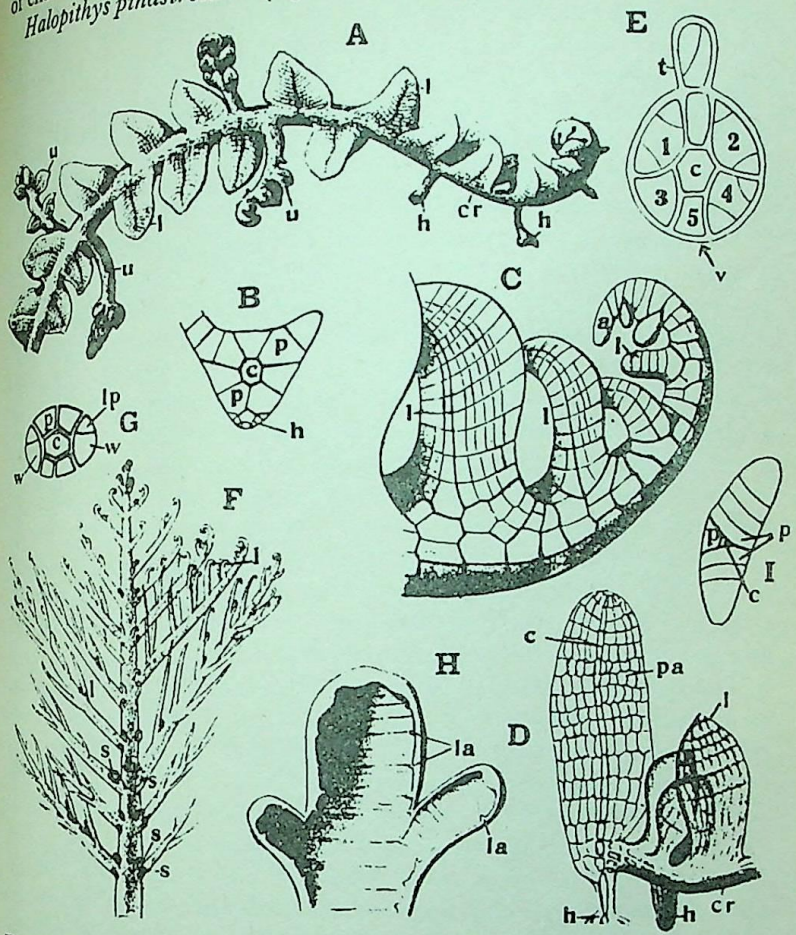

Fig. 211. A–D, I, *Leveillea jungermannioides* (Mart. & Her.) Harv.; A, habit; B, transverse section of prostrate axis; C, apex of long shoot; D, early stage in development; I, transverse section of young "leaf". E, F, *Halopithys pinastroides* (Gmel.) Kütz.; E, transverse section of apex of shoot (*1–5*, pericentrals); F, habit. G, H, *Kützingia canaliculata* (Grev.) Sonder; G, transverse section of apex of axis; H, apex of a shoot. *a*, apical cell; *c*, central cells; *cr*, prostrate axis; *h*, hapteron; *l*, laterals of limited growth; *la* (in H), endogenous laterals; *lp*, lateral pericentrals; *p*, pericentrals; *pa*, primary axis; *s*, secondary branch; *u*, shoots of unlimited growth; *v*, ventral side of thallus; *w*, part of lateral pericentral forming the wing. (After Falkenberg.)

Rytiphloea tinctoria (fig. 212 K; (15) p. 180, (189), (192) p. 438; cf. also (6) p. 106) are, however, richly branched Atlantic and Mediterranean perennials. The axes, which are cylindrical (fig. 211 F) in the former,

[1] *Rytiphloea pinastroides* C. Ag. ((276) pl. 85).

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but slightly flattened in the latter, have inrolled apices and bear a row of dorsal trichoblasts (fig. 211 E; *t*) on the younger parts. The two rows of endogenous laterals (*l*) are produced in pairs from two successive segments and form an acute angle with one another; the first two secondary branches (*s*) in *Halopithys* arise close to the parent-axis. The older parts develop an extensive parenchymatous cortex.

Like other Amansieae these two genera possess 5 pericentrals (fig. 211 E), the two first formed (*1*, *2*) lying on the convex (dorsal) side of the inrolled apex. A narrow two-layered wing is formed in *Rytiphloea* immediately behind the apex by division of the dorsal and dorso-lateral pericentrals (cf. fig. 212 F, G). Such a wing is more strongly developed in other Amansieae, as for instance in *Amansia* ((6) p. 108, (192) p. 407), where the cells of the two layers alternate (fig. 212 I, *w*) and those of adjacent segments become linked by secondary pit-connections. In *A. multifida* (fig. 212 B) the endogenous laterals (*l*) emerge in two alternating rows from between the two layers of the broad wings, the first segment of the lateral extending to the edge of the wing and producing only a dorsal and a ventral pericentral. The wings on these laterals lie in the same plane as those of the parent-axis and are continuous with the latter. In later stages exogenous adventitious fronds arise irregularly along the median line of the main axis (14). *A. multifida* thus represents a further elaboration of the condition found in *Rytiphloea*, and both differ essentially from *Halopithys* only in the development of wings.

The mature plants of *A. glomerata* (fig. 212 A; (192) p. 416) present an appearance very different from that of *A. multifida*. A robust terete stalk (*s*) bears on one side a number of dense leafy rosettes (*r*), consisting of flattened branch-systems which are placed edgewise. These "leaves" have the same structure as the thallus of *A. multifida*, although with broader wings and shorter laterals. The young plant closely resembles one of these "leaves" and from it the later ones arise exogenously, being homologous with the adventitious laterals of *A. multifida*. The rosettes are sympodia, each member of which arises adventitiously from the base of the preceding one. When a "leaf" originates, the adjacent cells of the axis develop a cortex (fig. 212 H, *co*), a process which advances basipetally and leads to the production of a thick rib (fig. 212 I, *co*) overlapping onto the wings. The peripheral parts of the latter slowly disorganise and in this way the terete stalk is formed. The two species of *Amansia* are widely distributed in warmer seas.

Diverse other Amansieae show much the same structure as *A. multifida*. In *Lenormandia* ((2) p. 1099, (192) p. 456, (270) pl. 2) the wing is one-layered owing to dovetailing of the two series of cells and there are no endogenous branches, secondary fronds (fig. 212 L, *sf*) arising exogenously and adventitiously from the margin. *L. marginata* ((277) pl. 235) and other species are known only from Australia. *Osmundaria*

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prolifera Lamour. (*Polyphacum proliferum* Ag. (192) p. 469, (277) pl. 188) is distinguished by the numerous small adventitious shoots covering the surfaces of the flat cartilaginous fronds. *Kützingia* (fig. 211 H; (192)

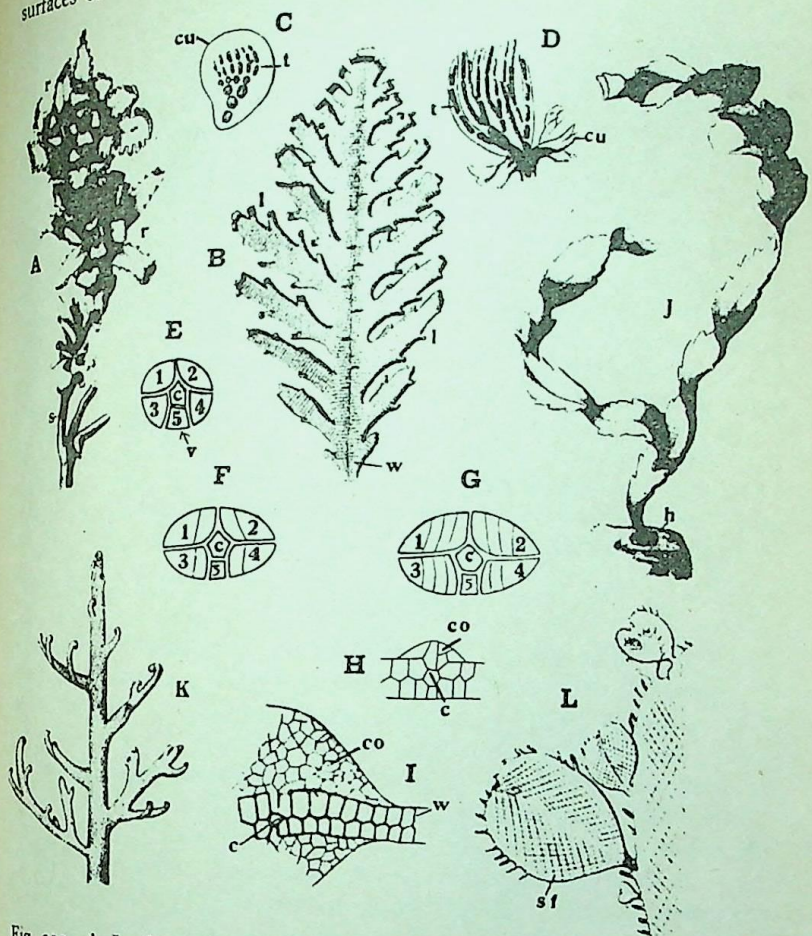

Fig. 212. A–I, *Amansia*; A, E–I, *A. glomerata* C. Ag.; B–D, *A. multifida* Lamour. A, B, habits of the respective species; C, young and D, older trichoblasts; E–G, transverse sections at successive distances behind the apex, illustrating the mode of wing-development; H, I, two stages in formation of midrib. J, *Vidalia volubilis* (L.) J. Ag., habit. K, *Rytiphlœa tinctoria* (Clements) C. Ag. L, *Lenormandia marginata* Hook. et Harv., with secondary fronds (*sf*). *c*, central cell; *co*, cortex of midrib; *cu*, cuticle; *h*, hapteron; *r*, rosettes; *s*, cylindrical axis; *t*, trichoblast; *w*, wing. (K after Ambronn; the rest after Falkenberg.)

p. 450, (270) pl. 9) differs from other Amansieae in the possession of 6 pericentrals (fig. 211 G), the one-layered wing being formed by division of the lower part (*w*) of the lateral pericentrals (*lp*) and exhibiting cortex-formation at an early stage. The older parts develop a coarse midrib which remains as a stipe after the wings have worn away (cf. (277) pl.

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232). The endogenous laterals (fig. 211 H, *la*) are opposite, but many of them remain rudimentary.

Vidalia (fig. 212 J; (14), (79) p. 183, (192) p. 423) again has a similar structure, although more robust owing to the formation of a few-layered cortex. Here several of the basal segments of the laterals, which appear as teeth along the margin, are included within the wings of the parent-axis. The frequent spiral twisting (fig. 212 J) is caused by wing-formation taking place also on the embedded parts of the laterals. Branching of the fronds is either due to further development of certain laterals (*V. spiralis* Lamour. = *Epineuron spirale* Harv. (270) pl. 9) or to adventitious branches (*V. volubilis*, fig. 212 J). The reproductive organs of the Australasian *V. spiralis* are formed on minute adventitious branches, while those of *V. volubilis*, occurring in the warmer seas of the Northern Hemisphere, are developed on certain more vigorous endogenous laterals.

Like *Halopithys* and *Rytiphloea*, both *Amansia* and *Vidalia* develop near the inrolled apices a single dorsal row of richly branched trichoblasts. It is characteristic of diverse species of the last three genera that, until the trichoblast is fully developed, the component cells remain small and constitute a compact pyriform group (fig. 212 C) enveloped by a "cuticle" (*cu*); as the cells elongate, the latter is ruptured, though parts of it persist at the base (fig. 212 D, *cu*).

(*d*) *Dasyaceae*

The few filiform genera belonging to the Dasyaceae are essentially distinguished from the Rhodomelaceae by the sympodial branching of the principal axes ((50) p. 316, (192) p. 609, (350) p. 108, (547) p. 33, (592) p. 224). A lateral, arising either from the basal (*Dasya*, fig. 213 F; *Dasyopsis*) or from the second or third (*Heterosiphonia*, fig. 214 D) segment of the previous generation, continues the growth of the axis, while the upper parts of the successive units of this sympodium (*1*, *2*, *3*, etc.) are deflected to one side and develop as branched uniseriate apparent laterals (pseudolaterals (*pl*) of Rosenberg) of limited growth; although different in origin, the latter resemble the pigmented trichoblasts of certain Rhodomelaceae. In *Dasya* (fig. 213 A, F) the pseudolaterals are spirally arranged, but in *Dasyopsis* (fig. 214 A) and *Heterosiphonia* (fig. 214 D) they are distichous and the plants have a pinnate habit. The pseudolateral usually produces a branch adaxially from every second segment (fig. 214 D, *br*), while in *Dasya* and *Dasyopsis* the laterals of the second order are abaxial; all the branches of the pseudolateral lie approximately in the same plane.

The sympodial axes (figs. 213 F; 214 D, *sa*) develop a polysiphonous structure throughout, while in *Heterosiphonia* the three basal segments of the pseudolaterals likewise become polysiphonous.[1] *Dasya* (fig. 213 E) and *Dasyopsis* possess 5 pericentrals, which develop in a

[1] According to Falkenberg ((192) p. 169) the basal segment may also become polysiphonous in *Dasya*.

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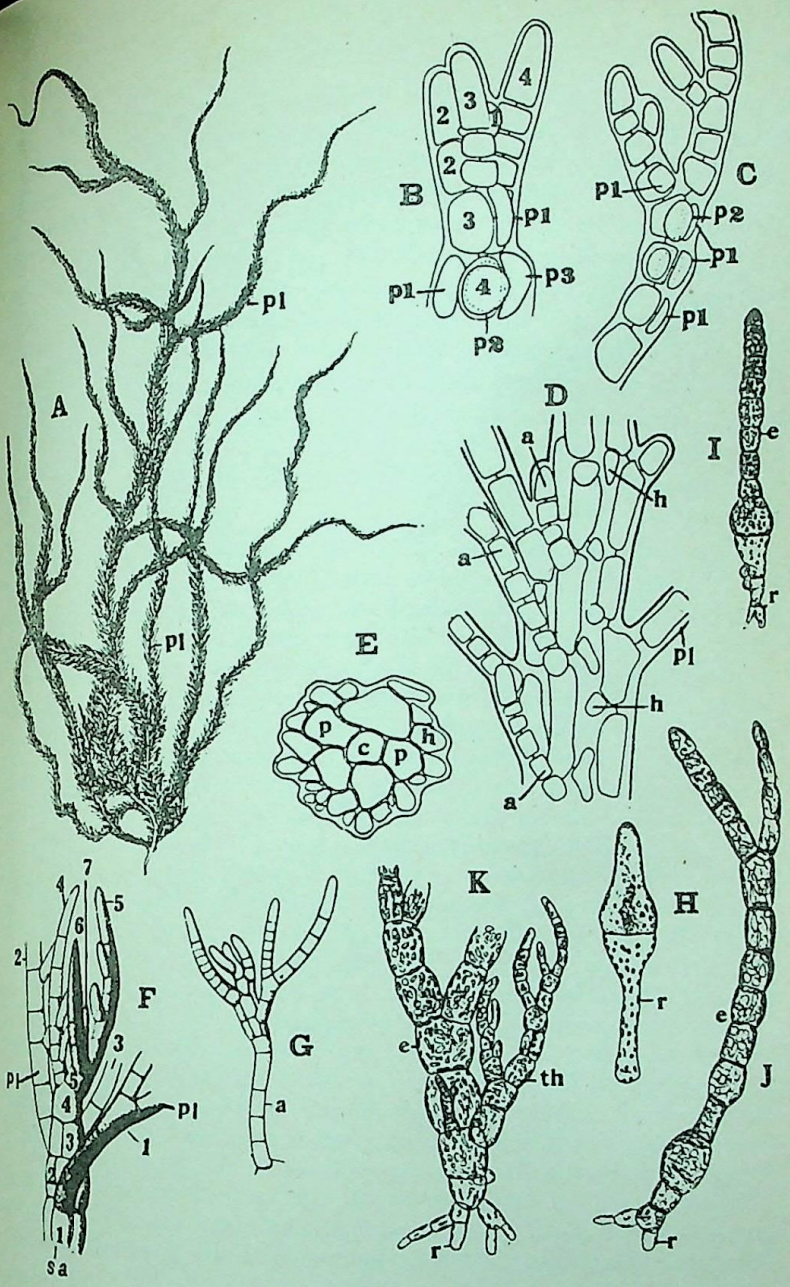

Fig. 213. *Dasya*. A–G, *D. pedicellata* Ag.; A, habit; B, C, F, apices showing details of branching, the successive axes numbered in B and F; D, part of an older axis; E, transverse section; G, adventitious lateral. H–K, *D. arbuscula* (Dillw.) Ag., successive stages in development. *a*, adventitious branches; *c*, central cell; *e*, erect primary axis; *h*, cortical threads; *p1*, *p2*, etc., pericentrals; *pl*, pseudolaterals; *r*, rhizoid; *sa*, sympodial axis; *th*, beginning of mature thallus. (A after Taylor; B–E after Rosenberg; F, G after Falkenberg; H–K after Killian.)

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sequence different from that of Rhodomelaceae (fig. 213 B, C), the first (*p1*) to one side of the pseudolateral, the second (*p2*) just below it, the third (*p3*) to the left of the second, and so on; the fifth is small and sometimes suppressed. *Heterosiphonia*, in which the number of pericentrals varies, on the other hand, for the most part develops them in the same way as in Rhodomelaceae. In *H. Berkleyi* Mont., a widely distributed Antarctic form, the larger axes are flattened owing to great enlargement of two opposite pericentrals. The branches of unlimited growth are for the most part (always in *Heterosiphonia*, fig. 214 D, *br*) constituted by the first branch of a pseudolateral. Adventitious laterals, especially plentiful in *Dasya arbuscula*, originate from the upper ends of the pericentral cells (fig. 213 D, *a*) and sometimes also from the cortex (cf. below); they usually remain monosiphonous (fig. 213 G).

In many species branched cortical threads, emerging from small cells cut off obliquely from the lower ends of the pericentrals (fig. 213 D, *h*) and linked by pit-connections both with one another and with the latter, give rise to a more or less thick cortex (figs. 213 E; 214 C, *h*); in *Heterosiphonia* (fig. 214 E, *h*) they grow both upwards and downwards. Such threads also arise from the basal cells of the pseudolaterals and of the adventitious branches. In *Dasyopsis* ((547) p. 54) the mother-cells of the cortical threads become very large (fig. 214 B, C, *h*) and penetrate between the pericentrals so as to obscure the primary structure. This accounts for the frequent denial ((192) pp. 37, 665, (726) p. 128) of the presence of pericentrals in this genus.

The early development of *Dasya* ((129) p. 496, (173) p. 253, (339) p. 225, (694) p. 363, (695) p. 9) is essentially like that of *Callithamnion* (fig. 213 H, I). Branching (fig. 213 J) sets in early, but both primary axis and branches remain uniseriate. The mature thallus (fig. 213 K, *th*) arises at a later stage from the original spore-body.

The species of Dasyaceae are largely sublittoral forms which favour warmer seas, although a number are to be found in temperate waters. *Dasya arbuscula* ((276) pl. 224) is probably the most widely distributed British species, while the much larger *D. pedicellata* Ag. (*D. elegans* (Mart.) Ag. (272) p. 60) is found on the warmer Atlantic shores of Europe and North America, as well as in the West Indies and the Mediterranean. A common North European form is *Heterosiphonia plumosa* (Ellis) Batt. (*Dasya coccinea* Ag. (276) pl. 253; *H. coccinea* Falkenb.). *Dasyopsis plumosa* is known from the North Pacific.

The Dasyaceae also include *Dictyurus* and *Thuretia*, which possess reticulate thalli, comparable to those of Delesseriaceae (p. 539); the former is found in the warmer parts of the Atlantic and Indian Oceans, the latter in Australian seas. In *Dictyurus* ((1) p. 17, (50) p. 327, (192) p. 675) a creeping system gives rise to terete upright axes (about 5 cm. high in *D. purpurascens*), each branch of which bears an elaborate sack-like network (fig. 215 A) in the form of a spiral veil. The basic structure is like that of other Dasyaceae. The sympodial

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axes possess 4 pericentrals (fig. 215 D, *m*), two segments to each joint (*cf. Heterosiphonia*), and the pseudolaterals are distichously arranged (fig. 215 C, *1–6*); they soon drop off on the lower parts of the erect axes (fig. 215 A, *m*) which become invested with a thick cortex.

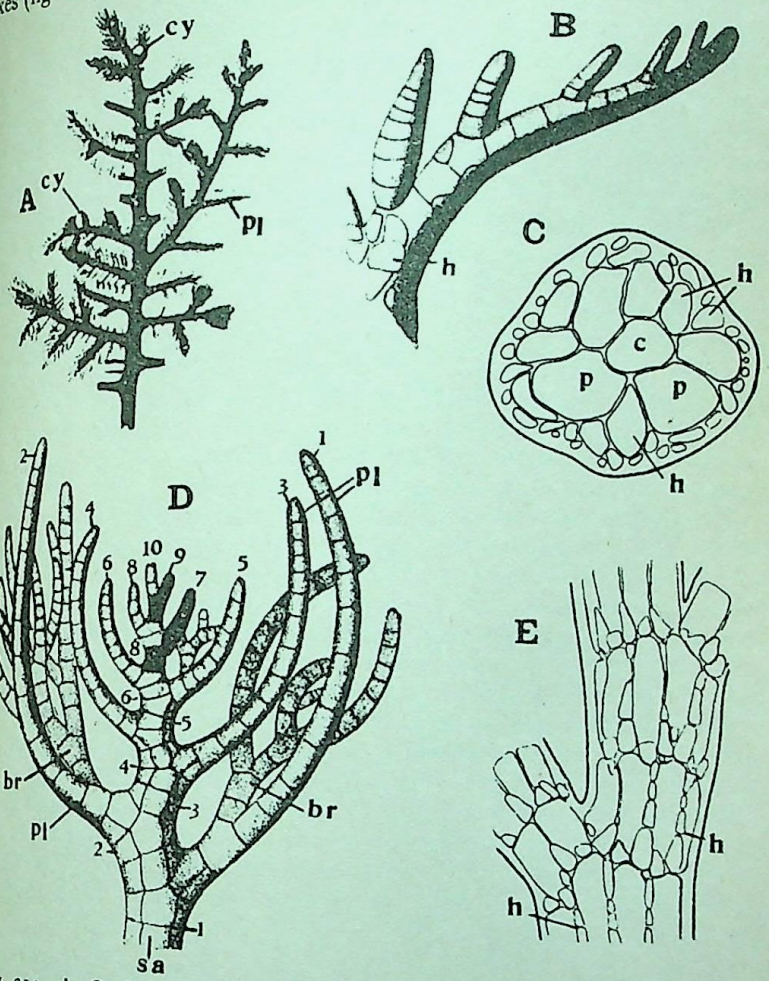

Fig. 214. A, C, *Dasyopsis plumosa* (Bail. & Harv.) Schmitz; A, habit; C, transverse section. B, *D. plana* (C. Ag.) Zanard., apex of a pseudolateral. D, *Heterosiphonia Wurdemanni* Bailey, apex of a shoot, the successive segments of the sympodium numbered. E, *H. plumosa* (Ellis) Batt., older part of a branch. *br*, branch; *c*, central cell; *cy*, cystocarp; *h*, cortical threads; *p*, pericentrals; *pl*, pseudolaterals; *sa*, sympodial axis. (C, E after Rosenberg; the others after Falkenberg.)

In the region of the net each pseudolateral branches abundantly in the horizontal plane (fig. 215 C, *pl*) so as to occupy about half the circumference of the axis; the first ramifications lead to the formation of four sympodial branch-systems (fig. 215 B, *i–iv*), their uniseriate

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pseudolaterals tending to be pinnately disposed. Net-formation commences, before there is any wide separation of the individual branches (fig. 215 E), by the abundant outgrowth from the cells of adjacent threads of processes (*p*) which grow towards one another and fuse at their tips (*f*). Such connections are established not only between the diverse laterals of each sympodial branch-system, but also along the margins, where two such systems meet (i.e. in fig. 215 C between *1* and *2*, *3* and *4*, etc. and, on the reverse side, between *2* and *3*, *4* and *5*, etc.). The close spiral thus constituted (fig. 215 D) is drawn out as the axis stretches (cf. fig. 215 J), but, prior to this, the upwardly curved tips occupying the edge of each branch-system become connected with the under surface of the next higher coil of the spiral. The network thus encloses an uninterrupted spiral cavity.

In *Thuretia* (fig. 215 F; (192) p. 668) there is only one segment to each joint of the sympodium and, in the principal axes, the polysiphonous structure is soon obscured by cortication (cf. *Dasyopsis*). In *T. quercifolia* (*Dictyurus quercifolia* J. Ag.) the lowest lateral of the distichous primary pseudolaterals (fig. 215 G, *pl*) gives rise to a secondary sympodium bearing numerous uniseriate pseudolaterals (*sl*) adaxially in two rows. Successive secondary sympodia follow closely upon one another so that their laterals project over those of the next youngest sympodium, with which connections are established at fairly regular intervals (fig. 215 H, *f*) in the same way as in *Dictyurus*. The elaborate network thus constituted consists of two or more interconnected systems. Occasional secondary sympodia develop into the lobes of the flat, rather spongy nets (fig. 215 F) of *T. quercifolia* ((277) pl. 40), which may reach a length of 20–25 cm. *T. teres* Harv. ((277) pl. 191) has cylindrical nets.

Brief mention may be made of *Halodictyon* ((54) p. 140, (192) p. 692, (478) p. 392), a genus of uncertain position, with a number of species in warmer seas. The plants consist of a branched network composed of cylindrical cells which are free at the margins (fig. 215 I); a polysiphonous structure appears only in the fertile parts. The apex of the net is occupied by a small-celled meristem, the segments of which rapidly lengthen and separate. *H. mirabile* Zanard. ((762) pl. 5) occurs in the Mediterranean.

The typical Dasyaceae have often been regarded ((192) pp. 681, 699, (339) p. 265, (387) p. 123) as the most primitive of the Rhodomelaceae, while Oltmanns ((502) p. 336) looks upon them as specialised (reduced) forms and seeks the origin of Rhodomelaceae among *Antithamnion*-like types. Rosenberg ((547) p. 83) concludes that the Dasyaceae have more in common with the Delesseriaceae than with the other two families of Ceramiales (cf. also p. 720). There is much that speaks in favour of Falkenberg's view, since the great resemblance of the pseudolaterals to the pigmented trichoblasts of the less specialised Rhodomelaceae cannot be denied; moreover, the origin of polysiphonous branches from the pseudolaterals recalls their development

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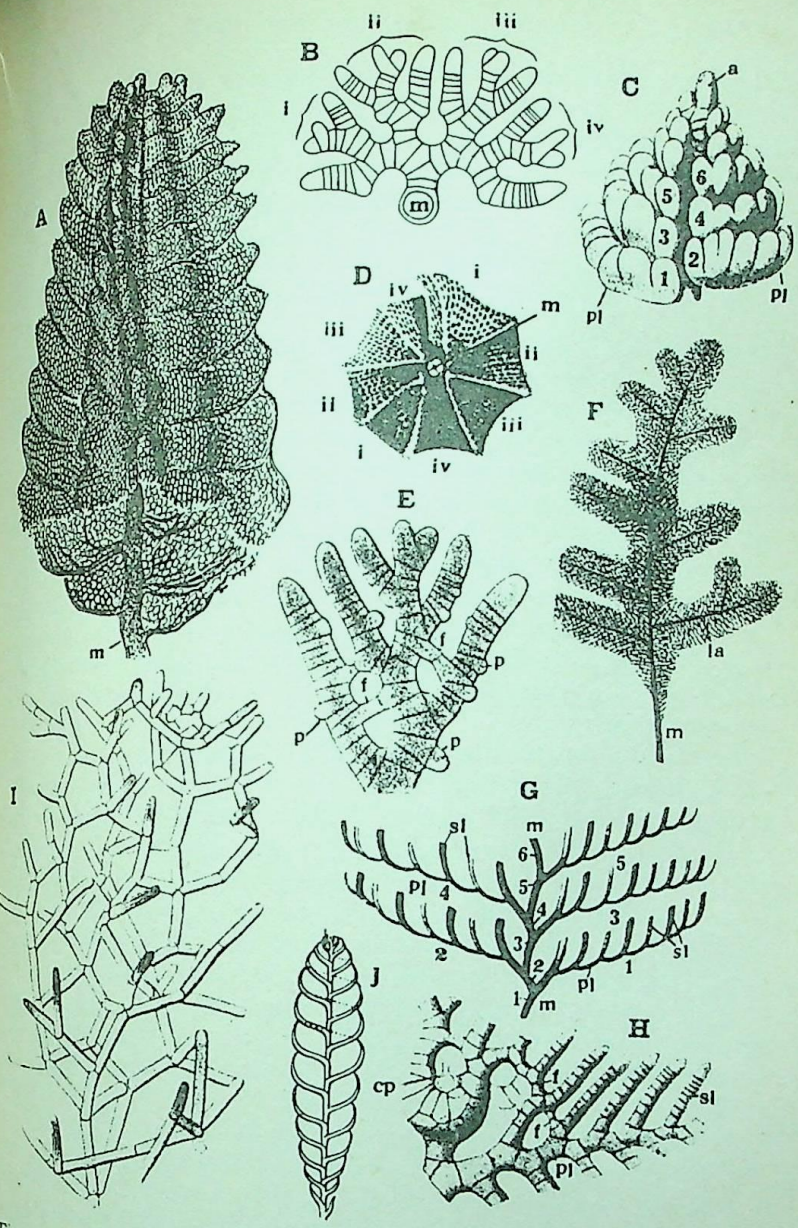

Fig. 215. A–E, J, *Dictyurus purpurascens* Bory; A, habit, part of the net removed at the base; B, young lateral sympodium, *i–iv* successive branch-systems; C, apex of axis showing distichous arrangement of pseudolaterals (*1–6*); D, apex of axis from below, *i–iv* correspond to *i–iv* in B; E, emission of processes (*p*) and formation of network; J, diagram to show mode of spiral union of lateral sympodia. F–H, *Thuretia quercifolia* Decsne; F, habit; G, diagram to show branching of primary pseudolaterals (*pl*); the two rows of secondary laterals (*sl*) indicated by the light and dark shading, *1–6* the successive joints of the sympodial axis; H, basal part of older lateral sympodia, with carpogonium (*cp*). I, *Halodictyon mirabile* Zanard., part of net. *a*, apical cell; *f* (in E and H), point of fusion of processes (*p*); *la*, lateral axis; *m*, axis; *pl*, pseudolaterals; *sl*, secondary laterals. (After Falkenberg.)

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from the trichoblasts in many Rhodomelaceae. On the other hand, it is difficult to regard the sympodial structure of Dasyaceae as primitive, nor are any traces of it to be found in Rhodomelaceae. The facts indicate that the former constitute an independent evolutionary line from an ancestry, common with that of the other three families of Ceramiales.

12. Parasitic Florideae

The numerous epiphytic Florideae are for the most part only attached superficially to their substratum. A certain number, however, exhibit a more intimate relation, either in their restriction to definite "hosts" ((226) p. 249, (618) p. 156) or in the possession of an endophytic attaching system, which penetrates more or less deeply into the substratum (701) and often causes some destruction of the adjacent cells; this is well exemplified by *Polysiphonia fastigiata* (p. 548). There is, however, little evidence of actual parasitism in such Florideae which are clearly well equipped for a holophytic existence, and the uptake of nutriment, if any, cannot be considerable. Tobler ((701) p. 85) points out that *P. urceolata* is found on parts of *Laminaria*, where there is an accumulation of organic detritus, and takes this as an indication of saprophytism.

Better instances of parasitism are afforded by those Florideae which are not only deeply anchored in their host, but also exhibit vegetative reduction as compared with their immediate allies. Examples are afforded by *Ceratocolax* (Phyllophoraceae), *Ricardia* and *Janczewskia* (Rhodomelaceae). *Ceratocolax Hartzii* ((157) p. 369, (425) p. 110, (554) p. 34, (558) pp. 545, 608, (561) p. 29) forms branched pink-coloured tufts (fig. 216 A, B) on *Phyllophora Brodiaei*. The degree of penetration of the host varies; sometimes the medulla is invaded and some of its cells killed, whilst in other instances (fig. 216 C) the parasite merely spreads beneath the "cuticle", sending haustoria into the walls of the underlying cells. Greater reduction is seen in *Callocolax neglectus* Schmitz (Callymeniaceae; (29) p. 316, (389) p. 31), which forms minute white growths on *Callophyllis laciniata*.[1]

The mature individuals of *Ricardia Montagnei*[2] ((54) p. 74, (171) p. 211, (503) p. 484), a close ally of *Laurencia* upon which it is usually found, appear as elongate or pyriform, bright red, hollow vesicles (fig. 216 H) of about the size of a pin's head; they have a several-layered wall and are anchored by an elongate rhizoid (*r*) which penetrates deeply into the tissues of the host. The spores germinate ((339) p. 230, (387) p. 95) within the apical depression of the latter (cf. p. 557

[1] Chemin ((129) p. 437) suggests that *Callocolax* may merely be an abnormal development of the host-plant.

[2] There is difference of opinion whether the Californian *R. saccata* (J. Ag.) Kyl. is a distinct species (cf. (404) p. 43, (613) p. 60). Other parasitic Rhodomelaceae are *Pleurostichidium* (292) and *Sporoglossum* ((405) p. 57).

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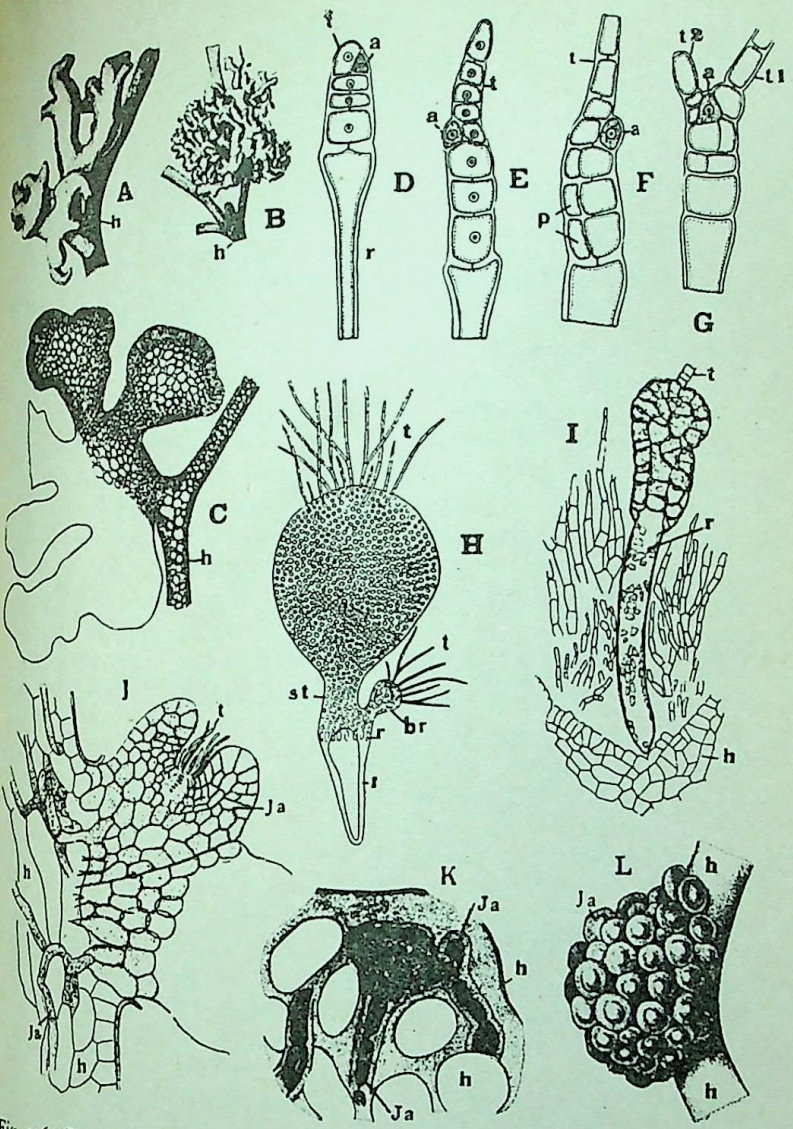

Fig. 216. Parasitic Florideae. A–C, *Ceratocolax Hartzii* Rosenv.; A, B, two types of growths on *Phyllophora Brodiaei* (*h*); C, section of tetrasporic plant. D–H, *Ricardia saccata* (J. Ag.) Kylin; D–G, early stages in development; H, considerably older stage. I, *R. Montagnei* Derb. & Sol., young germling in apical depression of *Laurencia*. J–L, *Janczewskia verrucaeformis* Solms-Laubach; J, vertical section of a young thallus; K, early stage in development of the parasite; L, habit. *a* (in D–G), apical cell of mature axis; *br*, branch; *h*, host; *Ja*, *Janczewskia*; *p*, pericentrals; *r*, rhizoids; *st*, stalk; *t*, trichoblasts. (A–C after Rosenvinge; D–H after Kylin; I after Killian; J, K after Falkenberg; L after Solms-Laubach.)

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and fig. 216 I), and the germlings attain a certain size before the rhizoid (*r*) begins to pierce the underlying tissue. At the four-celled stage (fig. 216 D) a three-sided apical cell (*a*) is cut out on one side of the top cell, the rest of which gives rise to a trichoblast (*t*). The underlying cells form pericentrals (fig. 216 F, *p*) and produce the basal stalk (fig. 216 H, *st*), the lowest cells of which may grow out into rhizoids (*r*). The mature vesicle is formed by the apical cell, which divides like that of *Laurencia* (p. 558), each segment producing a trichoblast; secondary vesicles (fig. 216 H, *br*) may arise from the lower cells of the stalk. In cultures the germlings fail to develop beyond a certain stage, and this is regarded ((339) p. 231) as evidence of incapacity for a further autotrophic existence. A comparable degree of parasitism is exhibited by the Antarctic *Colacodasya inconspicua* (Reinsch) Schmitz ((192) p. 658, (405) p. 65) which is parasitic on species of *Heterosiphonia*.[1]

Most species of *Janczewskia* ((54) p. 71, (192) p. 255, (487) p. 83, (616) p. 8, (651), (727) p. 348)[2] occur in temperate seas as minute cushions (fig. 216 L, *Ja*) on *Chondria* and *Laurencia*. The usual colour of *J. verrucaeformis* is pale yellow (cf. however (616) p. 8), and the individuals are probably for the most part heterotrophic; several species are practically white. The cushions consist of a number of short, more or less coalescent fronds (fig. 216 L; less markedly fused in *J. tasmanica* Falkenb.), having a similar structure (fig. 216 J) to those of *Laurencia* and arising from a system of endophytic filaments (fig. 216 J, K, *Ja*), which are probably formed first; their cells are stated to be joined by pit-connections with those of the host. The latter does not appear to be weakened, although there is often a sharp bend at the point of attack.

Gonimophyllum ((27), (382) p. 95, (405) p. 34, (487) p. 82, (619) p. 394, (638) p. 50), parasitic on *Cryptopleura* and other Nitophylleae, shows similar features. The minute, pale pink leaflets arise in tufts from the hypertrophied tissue of the host, within which lie the endophytic threads. Both here and in *Janczewskia*, although the capacity to produce some photosynthetic pigment is not altogether lost, the usual pale colour, the minute size of the individuals, and the deep penetration of the endophytic system, imply a considerable degree of parasitism. In *Polycoryne* ((382) p. 62, (405) p. 36, (619) p. 395, (638) p. 52), closely allied to its host (*Myriogramme*), the thallus is needle-like.

A complete absence of photosynthetic pigments is found in *Choreocolax* and *Harveyella* ((656-8); see also (185), (424) p. 55), which appear to be cold-water forms of the Northern Hemisphere and are still of doubtful systematic position (p. 650). The cushions (fig. 217 A, *ch*), which form the visible part of the parasite and which are about as big as a cystocarp of the host, are white or brownish when old.

[1] The *Colacodasya* described by McFadden (439) is, according to Kylin ((404) p. 46), also one of the Rhodomelaceae and not a member of Dasyaceae.

[2] *Benzaitenia* (761) shows similar features.

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Choreocolax Polysiphoniae ((194) p. 6, (541), (658)) is found not uncommonly on *Polysiphonia fastigiata*, at the points of branching (fig. 217 A) and on the young antheridial branches. According to Richards ((541) p. 48) plants thus attacked are paler and less vigorous.

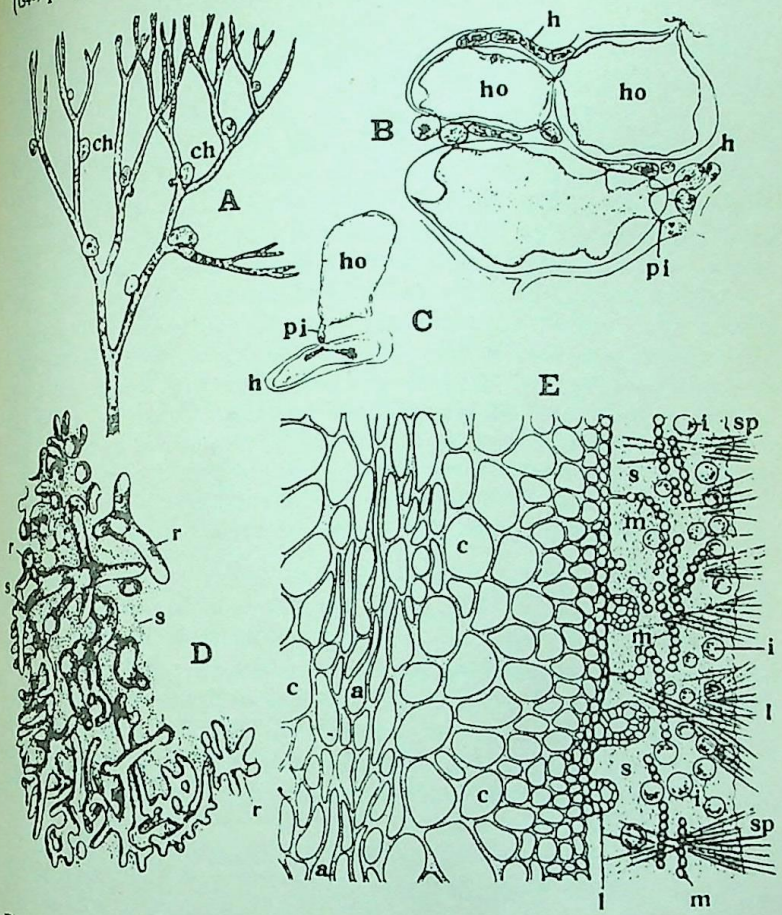

Fig. 217. A, *Choreocolax Polysiphoniae* Reinsch (*ch*) on *Polysiphonia fastigiata*. B, C, *Harveyella mirabilis* (Reinsch) Schmitz & Reinke, pit-connections (*pi*) between the cells of the parasite (*h*) and those of the host (*ho*). D, *Ceratodictyon spongioides* Zanard., transverse section of a branch; *r*, alga; *s*, sponge. E, *Thamnoclonium Treubii* van Bosse, longitudinal section of thallus; *a*, axial cells; *c*, cortex; *i*, isolated algal cells; *l*, lateral; *m*, moniliform chains formed by alga; *s*, matrix and *sp*, spicules of sponge. (A after Sturch; B, C after Rosenvinge; D after Askenasy; E after Weber van Bosse.)

The commonest species of *Harveyella* is *H. mirabilis*[1] which is parasitic on *Rhodomela subfusca*; a second species, *H. pachyderma* (Reinsch)

[1] *Choreocolax mirabilis* Reinsch; *C. albus* Kuck. (356). For other literature see (87) p. 292, (112), (538) p. 28, (558) p. 494.

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Batt.,[1] parasitic on *Gracilaria confervoides*, is referred by Sturch ((658) p. 599) to a distinct genus, *Holmsella*, owing to differences in reproduction (p. 650). In both the endophytic filaments traverse the middle lamellae of the host (fig. 217 B, *h*) and their cells establish secondary pit-connections (*pi*) with those of the latter (*ho*), whilst in *Choreocolax* direct connection is made with the pits of the host. Actual penetration of the cells is infrequent ((657) p. 28). In *Harveyella mirabilis* the parts attacked hypertrophy and some of the resulting cells may become incorporated in the tissue of the parasite ((356) p. 986). In *Choreocolax* the endophytic threads sometimes give rise to secondary cushions.

These genera appear to be multiaxial, the medulla consisting of branching filaments, while the small peripheral cells of the cortex are arranged in rows. The cushions are covered by a gelatinous envelope which, in *Holmsella pachyderma*, is as thick as the cortex. Rosenvinge ((558) p. 495) records probable leucoplasts in the cells of *Harveyella*.

Little is known about the early development. The first growth in *Choreocolax* is stated to be external ((102) p. 51, (541) p. 51), the endophytic filaments arising secondarily. Sturch ((657) p. 30), on the other hand, suggests that the spores of *Holmsella* obtain access to the interior of the host through the crevices left after the escape of its spores. According to Chemin ((112), (129) p. 443) the spores of *Harveyella mirabilis*, when allowed to germinate on glass slides, develop phycoerythrin and produce a circular disc with radiating peripheral threads which are supposed to penetrate the host. This requires confirmation.

The highest degree of parasitism is probably realised in forms like *Colacopsis* (fig. 299 E–G; (192) p. 531,[2] (405) p. 61, (599) p. 452) and *Stromatocarpus* ((192) p. 185, (619) p. 395) (Rhodomelaceae), as well as *Choreonema* (Corallinaceae), in which the entire vegetative system is endophytic and the fructifying fronds alone appear above the surface of the host.[3] *Stromatocarpus* is found on *Polysiphonia virgata* at the Cape. In both the Rhodomelaceous genera the polysiphonous reproductive shoots contrast markedly with the uniseriate endophytic threads.

The vegetative parts of *Choreonema Thureti* ((455), (659) p. 53; *Melobesia Thureti* Thur. & Born. (652) p. 54, (692) p. 96; *Endosiphonia Thureti* Ardiss. (19) p. 451) are completely enclosed in the tissues of *Corallinas* in which no kind of deformation is produced. The presence of the parasite (fig. 161 B, *c*) becomes evident only when the superficial conceptacles are formed.[4] The branched endophytic threads consist of elongate cells which cut off two or three small elements; these have been regarded as arrested branches or as comparable to

[1] *Choreocolax pachyderma* Reinsch. Wilson ((747); cf. also (619), (729) p. 143) records on Californian *Gracilarias* a parasite, *Gracilariophila*, which probably belongs here (cf. (185) p. 230).

[2] As *Colaconema* (cf. p. 424, footnote).

[3] Cf. also *Gelidocolax* ((236) p. 340)..

[4] The lateral conceptacles figured by Harvey ((276) pl. 201) in *Corallina squamata* belong to *Choreonema*.

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the cover-cells of *Melobesia*. In *Melobesia deformans* Solms-Laubach ((652) p. 57; *Chaetolithon deformans* (Solms) Foslie), which attacks Southern species of *Corallina*, the infected segments become irregularly branched, and their tissue may proliferate to such an extent that only the apertures of the conceptacles of the parasite are left uncovered.

It is noteworthy that, among the more definite instances of parasitism among Florideae, host and parasite usually belong to the same order, often indeed to the same family (cf. (618), (619)). This specialisation is striking in view of the usual growth of seaweeds in dense communities, where a diversity of hosts is available. The frequent close affinity between the two organisms perhaps also accounts for the slight degree of damage to the host, since there is no good evidence of any marked mortality as a result of the parasitic attack.

Diverse instances are known of association between Florideae and sponges. One of the most striking is furnished by *Ceratodictyon spongioides* ((765); *Marchesettia spongioides* Hauck (285), (287)), a member of Gracilariaceae found in deep water in the Mediterranean and in the Indian and Pacific Oceans. The terete branches of the cartilaginous thallus ((21) p. 40, (446), (599) p. 388) anastomose to form a network, which is completely enclosed in the body of the sponge (*Reniera fibulata* O. Schm.); the latter also occupies the meshes (fig. 217 D, *s*), the fructifying branches of the alga alone projecting beyond the surface. Although the sponge can lead an independent existence, there is so far no evidence that the seaweed can do so (cf. also (597) p. 145).

Further examples are afforded by species of the Southern genus *Thamnoclonium* (Grateloupiaceae; (6) p. 18, (95) p. 163, (599) p. 514, (725), (727) p. 250). In *T. Treubii* (fig. 217 E) the axes with their many short branches (*l*) are entirely overgrown by the sponge (*s*). The superficial cells of the alga here produce unicellular processes, giving rise at their tips to chains of rounded cells (*m*), the outermost of which become detached and enlarge within the matrix of the sponge (*s*); the detached cells (*i*) contain a large chromatophore and grains of starch, while their vacuole is often occupied by a crystalloid.

Gall-like growths, which in part at least are possibly due to Bacteria (127, 589, 654), are not uncommon on certain red seaweeds. Such are the globular or irregular swellings, with or without pigment, found in *Cystoclonium purpureum*[1] ((109) p. 445, (589)) and the spherical or hemispherical galls occurring on the older fronds of *Ahnfeltia* ((252) p. 132, (558) p. 560, (591) p. 395); in the latter they consist of cortical tissue only, which undergoes progressive disorganisation from within outwards and, according to Chemin ((125) p. 343), Harvey ((276) pl. 288, fig. 3) shows such a gall in section. In *Cystoclonium* Rosenvinge ((558) p. 594)

[1] *Choreocolax Cystoclonii* Kyl. ((369) p. 127) may be identical with these growths ((558) p. 596).

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found no Bacteria within the galls, but in *Chondrus crispus* (109), where they cause perforations in the fronds, Chemin ((127) p. 321) states that another French worker (92) has succeeded in preparing bacterial cultures from them and in causing gall-formation by inoculation with the latter or with an extract of the tumours. The galls of *Rhodymenia palmata* are due to Copepods (24).

Chondrus is often attacked by the Pyrenomycete *Didymosphaeria marina* (Rostr.) Lind. (cf. also (768)). Diverse Chytridineae ((138) p. 39, (440) p. 76) and Phycomycetes (783) have been reported on Florideae.

13. Special Morphological and Biological Features

(a) *Light-reflecting Bodies*

Diverse Florideae, mainly inhabitants of warmer seas, show a blue or green iridescence ((36) p. 419, (37) p. 685, (187), (349), (444), (664)) when exposed to strong light, which is due to reflection of the shorter waves by bodies situated within the peripheral cells. The phenomenon is shown by *Chondria caerulescens* and certain other Ceramiales (species of *Callithamnion*, *Laurencia*, *Nitophyllum*, etc.), as well as by some Rhodymeniales (species of *Champia* (406) p. 303; *Chylocladia* and *Gastroclonium*); it is not recorded in the Northern species of the latter ((558) p. 578). The bodies causing iridescence are usually situated in the vacuoles and often in the main consist of protein (*Callithamnion*, Delesseriaceae), although those of *Laurencia* are stated ((197) p. 81) to be of the nature of tannins. In bright light (fig. 218 B) the bodies in question (*r*) are apposed to the outer walls, while the chromatophores (*c*) occupy the others; on transference to diffuse light (fig. 218 A) the relative positions are interchanged, the movement of the chromatophores being accompanied by amoeboid changes of shape.

In *Chondria caerulescens* ((37) p. 693, (266) p. 280, (349) p. 433, (444)) the light-reflecting bodies (fig. 218 E, *r*) consist of aggregates of yellowish granules which are readily soluble in potash and slowly dissolve in fresh water. Those of *Laurencia* ((197) p. 81, (266) p. 283, (713) p. 488) appear as large spheres which are sometimes confluent. For the most part, however, the bodies responsible for the reflection of the light are single, highly refractive masses, yellowish or milky white in colour and exhibiting a definite structure. Thus, in *Chylocladia kaliformis* ((37) p. 685) and *Gastroclonium clavatum* ((444) p. 662) they are lamellated, in the former with numerous small spherical bodies between the lamellae (cf. fig. 218 C). Berthold regarded the spheres as the actual reflectors.

The light-reflecting bodies of Delesseriaceae ((187) p. 807) have a similar structure. In strong light they become more and more opaque owing to an increase in the quantity of the spheres; in weaker light, on the other hand, the lamellate structure again becomes recognisable and by degrees the masses (fig. 218 B, *r*) break up into amoeboid portions which pass to the side walls (fig. 218 A). The spheres have been regarded as photosynthetic products laid down in a proteinaceous ground-

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mass. The iridescent bodies would, however, seem to be of diverse character and further study is necessary to elucidate their chemical nature (cf. also (197) p. 82).

In *Callithamnion* ((197) p. 75, (444) p. 660) the globular iridescent bodies are usually several in number; while in *Seirospora* ((197) p. 77) they are generally single; in neither instance do they show any structure. Iridescence, due to granular contents in the subepidermal cells, is also recorded in *Scinaia furcellata* ((37) p. 697, (226) p. 379, (266) p. 287), while the strongly refractive spherical bodies in the surface-cells of *Sphaerococcus coronopifolius* and *Plocamium coccineum* ((251) p. 264) appear to fulfil a similar light-reflecting rôle.

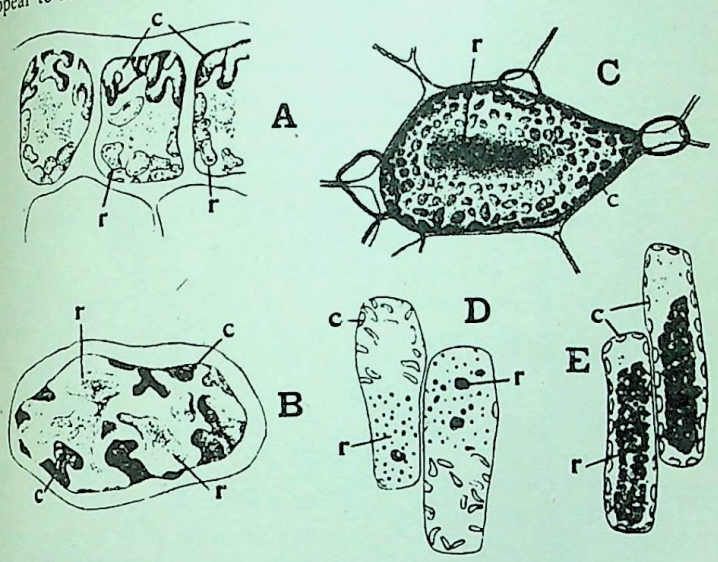

Fig. 218. Light-reflecting bodies. A, B, *Nitophyllum* sp.; A, surface-cells in section in light of moderate intensity; B, cell in surface-view in strong light. C, *Chylocladia reflexa* Lenorm., cell from the surface in strong light. D, E, *Chondria caerulescens* (Crouan) Falkenb., cells in vertical section, D in moderate, E in strong light. *c*, chromatophores; *r*, light-reflecting bodies. (A, B after Faber; C after Berthold; D, E after Mangenot.)

The possession of iridescent bodies has usually been regarded as ensuring protection against the injurious effects of strong insolation by partial reflection of the light. Several iridescent Mediterranean species are, however, inhabitants of grottoes and other shaded habitats ((197) p. 84) where such an explanation is inadequate. This suggests that the function of these bodies may vary.

(*b*) *Vesicular Cells*

Some Florideae bear, especially on the younger parts, small cells with a scanty protoplast and a prominent vacuole with highly refractive, homogeneous, and generally colourless contents. In certain species

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these vesicular cells are rich in iodine (iodine-cells; "ioduques" of Sauvageau (569) p. 32), the presence of which is shown by the blue colour assumed by starch-containing paper on contact with the seaweeds in question ((53) p. 79, (544)). Such cells are coloured deep brown by cyanin, which stains the ordinary cells blue. They are very charac-

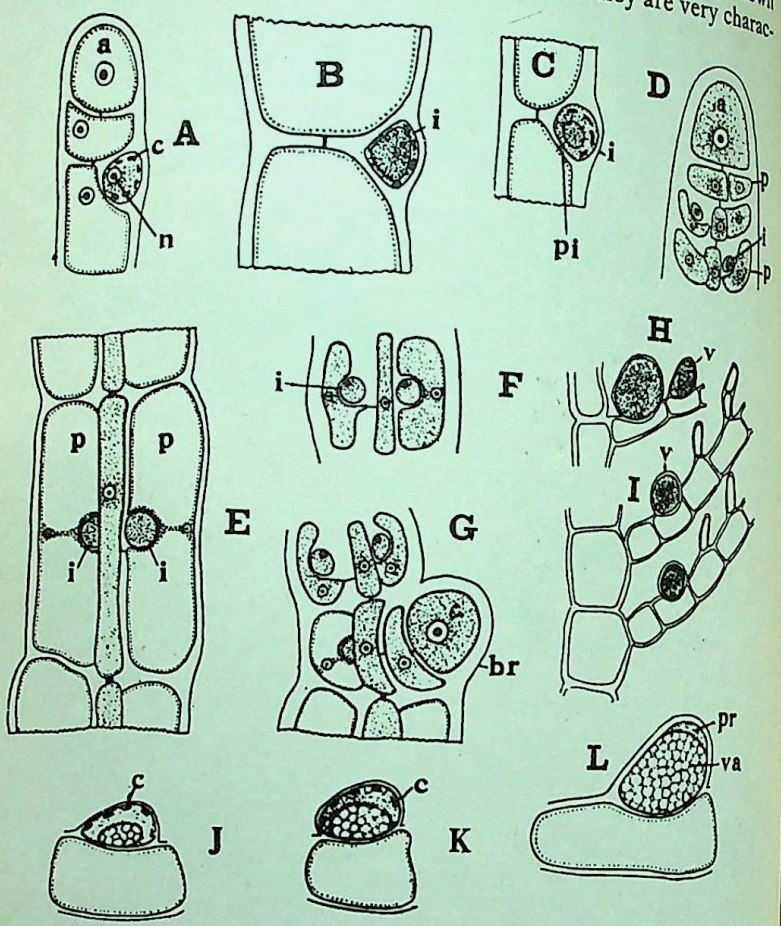

Fig. 219. Vesicular cells (after Kylin). A–C, *Trailiella intricata* (J. Ag.) Batt. D–G, *Falkenbergia Hillebrandii* (Born.) Falkenb. H–L, *Antithamnion plumula* Thur. *a*, apical cell; *br*, branch; *c*, chromatophore; *i*, iodine-cell; *n*, nucleus; *p*, pericentral; *pi*, pit-connection; *pr*, cytoplasm; *v*, vesicular cell; *va*, vacuole.

teristic of the Bonnemaisoniaceae (fig. 165 I, J, *v*; (79) p. 179, (121) p. 39, (251), (372), (390), (570)) and are also met with in certain Ceramiales (*Trailiella*, fig. 219 B, C, *i*; *Falkenbergia*, fig. 219 E, F, *i*); many of the species involved occur in Southern seas.

The distribution of the vesicular cells has already been described in *Bonnemaisonia asparagoides* (p. 482), where they show a blue fluorescence when viewed in reflected light, and it appears to be

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similar in *Asparagopsis* ((121) p. 39, (569) p. 14). Those of *Trailiella intricata* ((372) p. 4,[1] (373) p. 89, (602) p. 213) are small triangular structures situated at the top of each segment (fig. 219 B, C, *i*). In *Falkenbergia* ((385) p. 236; cf. also (569) p. 24) they are cut off on the upper side of the young pericentral (fig. 219 D, *i*), but, as the latter enlarges, they come to lie between it and the central cell (fig. 219 E, F, *i*) so that they were long regarded as vacuoles of the elongate pericentrals (*p*); the vacuoles in the iodine-cells of *Asparagopsis armata* are similarly stated (208) to be actual cells. The tetraspores and germlings of *Falkenbergia* contain no iodine (495), although vesicular cells appear at an early stage.

The iodine-cells contain an obvious nucleus (fig. 219 A, *n*), while a few chromatophores (*c*) may at first be present ((390), (602) p. 214). Sauvageau ((569) p. 31, (571), (573) p. 78, (574); cf. also (495)) was of the opinion that free iodine was contained in these cells, but the available evidence speaks for the presence of a compound ((116), (117) p. 139, (130), (385) p. 239, (388) p. 66). If material is placed in starch-solution with a little acetic or hydrochloric acid, the vesicular cells become surrounded by a blue halo, which is deeper in the presence of nitrites ((372) p. 4, (373) p. 90); this reaction is not obtained with young or old cells, nor at all times of the year (122), while in *Bonnemaisonia* it only appears if nitrites are present. The older vesicular cells collapse and liberate iodine without treatment with acid, which is believed ((155) p. 66, (156) p. 266, (388) p. 73) to be due to oxidases. These occur in considerable quantity in certain Red Algae ((241), (242), (388) p. 77, (534)); for peroxidases see (773).

The seaweeds under discussion contain considerable quantities of iodine (cf. also (344)), in *Trailiella* about 0·5 % and in *Bonnemaisonia asparagoides* about 0·3 % of the fresh weight, whereas the amount in other Rhodophyceae is much smaller ((388) p. 59). Kylin ((390) p. 219) is of the opinion that the ordinary cells contain alkali iodides, the presence of which is shown by the reddish needles appearing after treatment with cresyl blue ((385) p. 241, (388) p. 53, (443)), whereas the vesicular cells merely assume a greenish tint, ascribed to the liberation of free iodine. The function of these cells is still problematical, but there is some evidence that forms possessing them are avoided by animals; moreover, the excretion of iodine on the collapse of the older cells may prevent colonisation by epiphytes (cf. (384) p. 281, (602) p. 217).

Vesicular cells, which do not contain iodine, occur on the branchlets (figs. 185 B, *ve*; 219 H, *v*) of certain species of *Antithamnion* ((36) p. 516, (54) p. 53, (79) p. 181, (93) p. 373, (390) p. 222, (476) p. 64, (481), (569) p. 6, (601), (602) p. 202, (739) p. 67). In the mature cell (fig. 219 L) the protoplast (*pr*) forms an apical cap, while the contents of the vacuole (*va*) are coloured blue by cresyl blue. The osmotic value is higher than that of the vegetative cells (40). Sauvageau ((572) p. 8) concluded that these cells contained free bromine ("bromuques"), but this has been disputed ((384) p. 277, (390) p. 225) by Kylin, according to whom ((388) p. 71, (400) p. 36) very little of this element is present. Similar vesicular cells are

[1] Under the name of *Spermothamnion roseolum*.

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found in *Platythamnion* ((383) p. 51), in *Antithamnionella* ((572) p. 21), and in certain species of *Ceramium* (cf. (497) and p. 527), in one of which the storage of bromine has also been affirmed ((496); cf. however (384) p. 281).

(c) *Tendrils*

Diverse Florideae (*Asparagopsis hamifera*,[1] fig. 220 E; *Cystoclonium purpureum*; *Hypnea musciformis*, fig. 168 A, *t*; *Spyridia aculeata*, fig. 188 C; *Laurencia virgata* (612); *Acrosorium uncinatum*, etc.) possess curved, sickle-shaped laterals which, after contact with another branch of the same or of a foreign alga, can form one or more firm coils around it after the manner of a tendril (cf. especially (485)). In these laterals the outer tissues are often more markedly developed on the convex face (fig. 220 H) and branches, which commonly remain rudimentary till contact is established, are for the most part confined to that side; in *Hypnea* (fig. 220 H) and *Acrosorium uncinatum* the cells on the two sides differ in size. The tendrils of *Cystoclonium* ((104) p. 220, (291) p. 372, (440) p. 69, (558) p. 591, (742) p. 33) are long thin twisted structures (fig. 220 F), which can form 4–5 coils around the support, but more usually the curved tips are thicker than the part below (*Asparagopsis hamifera*, fig. 220 E, *t*; (121) p. 33, (265) p. 108; *Hypnea* (485) p. 240; *Ceramium hypnaeoides* (493)). The tendrils of *Asparagopsis hamifera* are laterals of limited growth and are richly stocked with reserve materials.

In *Hypnea* ((485) p. 244) and in *Calliblepharis lanceolata* ((104) p. 217, (110)), where certain of the long marginal proliferations act as tendrils, the tip curves after contact, thus decreasing the amplitude of the hook, while the apex resumes growth and forms a number of coils (fig. 220 D). Subsequently the cells on the inner surface elongate into attaching rhizoids (fig. 220 D, G, *s*), which are often thick-walled and commonly (*Hypnea*, *Acrosorium*) cohere in groups; the attaching system thus formed occupies all the surface-irregularities of the support. Nordhausen concluded that inrolling of the tendril and production of rhizoids is the result of a definite contact-stimulus. If a foreign alga is encircled, the latter exhibits no response, but when the tendril grasps another branch of the same alga both structures form rhizoids at the surface of contact and fusion ensues ((104) p. 218, (485) p. 247).

After contact the branches on the convex surface of the tendril develop and, in *Acrosorium uncinatum*, the hitherto small lobes upon them enlarge to normal dimensions ((485) p. 268). Subsequent rupture of the part behind probably often results in vegetative propagation ((485) p. 27). The large cells of *Griffithsia* ((428) p. 652) can put out rhizoids which, curving round other branches (fig. 185 H) or adjacent objects, give rise to new shoots which become detached.

[1] Also certain species of *Bonnemaisonia* (e.g. *B. californica* Gardner (88) p. 181, (236) p. 335, (387) p. 22), but not *B. asparagoides*.

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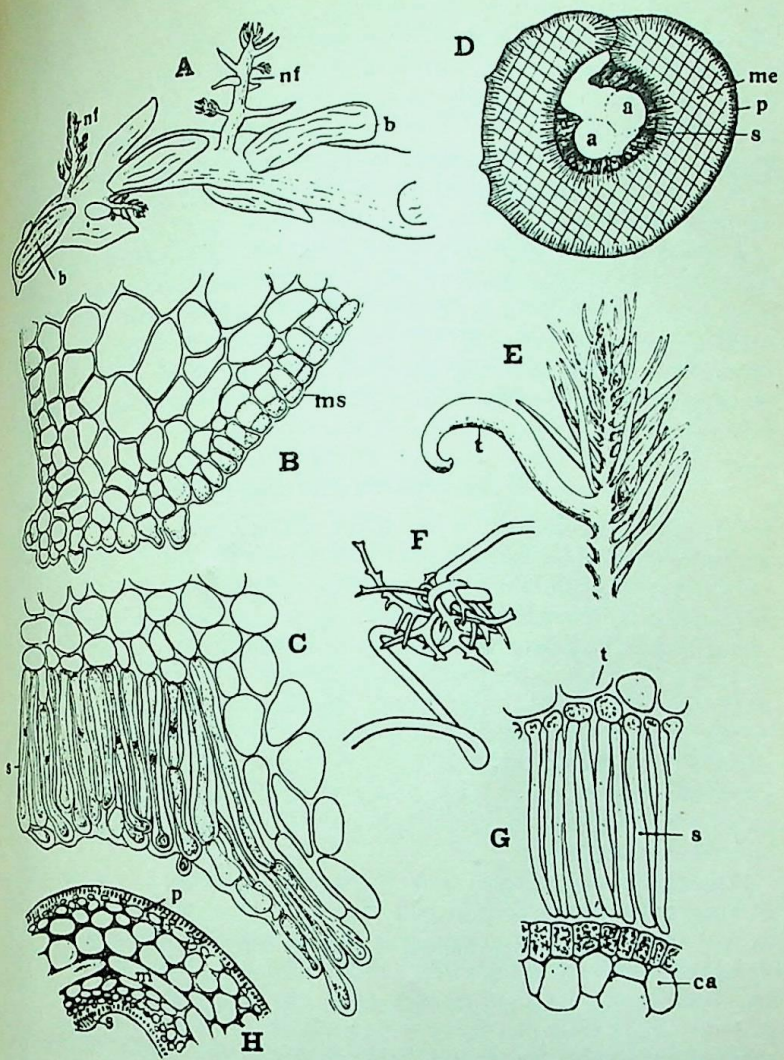

Fig. 220. A–C, *Asparagopsis armata* Harv.; A, prostrate shoot, with recurved branches (*b*) and new fronds (*nf*); B, tip of a recurved branch; C, the same, with the superficial cells (*s*) growing out as rhizoids. E, *A. hamifera* (Hariot) Okam., tip of a shoot, with tendril (*t*). D, G, *Calliblepharis lanceolata* Batt.: D, tendril enclosing two branches (*a*) of *Ahnfeltia plicata*, in transverse section; G, region of contact between tendril (*t*) and another branch of *Calliblepharis* (*ca*). F, *Cystoclonium purpureum* (Huds.) Batt., two tendrils coiled around one another. H, *Hypnea musciformis* (Wulf.) Lamour., longitudinal section of tendril showing unequal development of tissue on the two surfaces. *m*, axial thread; *me*, medulla; *ms*, meristematic cells; *p*, photosynthetic tissue; *s*, tissue at surfaces of contact; *t*, tendrils. (A–C after Svedelius; D, F, G after Chemin; E after Taylor; H after Nordhausen.)

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Recurved branches (fig. 220 A, *b*), representing laterals of limited growth and aiding in secondary attachment and vegetative propagation, are found in *Asparagopsis armata*, although these structures are not capable of twining ((141) p. 149, (679) p. 10). After contact with a foreign body the cells at the tip grow out into long rhizoids (fig. 220 C) which form an adhesive disc (cf. *Plocamium*, p. 492). The lateral of unlimited growth, situated opposite the hook (fig. 220 A, *nf*), develops vigorously after contact, and this is often accompanied by detachment of the whole system.

Fusions between branches of the same or of different species of Red Algae are not infrequent in forms lacking definite tendrils ((62) p. 114, (104) p. 214, (454), (700) p. 301). It is again associated with rhizoid-development, which is reciprocal only when parts of the same alga are concerned. Such phenomena have been reported in *Calliblepharis ciliata*, *Lomentaria clavellosa*, species of *Rhodymenia*, *Nitophyllum punctatum*, etc.

(*d*) *Wound-healing and Regeneration*

In Florideae possessing a compact thallus wounds are healed by active division of the uninjured cells to form a kind of callus ((367) p. 152, (451) p. 9). Decapitated plants of *Polyides* and *Furcellaria* ((170) p. 20) produce, from the medullary cells at the exposed surface, vertical threads which in part originate from the more deeply situated cells (cf. Fucales, p. 361) and give rise to a small-celled cortex. From such wound-tissues adventitious branches often arise. In Delesseriaceae ((75) p. 12, (337) p. 269, (367) p. 156) quite small pieces can proliferate from the midrib. According to Malkovsky ((441) p. 128) small fragments of *Nitophyllum punctatum* regenerate readily, new branches arising from the apical end and from uninjured marginal cells, whilst the basal end merely forms an extensive callus.

Among Rhodomelaceae ((192) p. 74, (698)) damage to the apex results in outgrowth of the central cell into a new polysiphonous axis. Both in this family and in Ceramiaceae regeneration easily takes place from detached fragments which first produce rhizoids, usually from the basal end ((119) p. 9, (447), (697) p. 563, (730)); in *Griffithsia* ((326) p. 124, (428) p. 673) single cells can form a new plant. Polarity is in general well marked, although Schechter (576) records reversal in fragments of *Griffithsia* after 24 hours' subjection to a moderate centrifugal force (cf. also (575)); diminished illumination ((697) p. 543) causes the apex of many Florideae to grow out into rhizoid-like threads. In *Ceramium* a new axis often arises from cortical cells. Damage to or death of intermediate cells in *Bornetia* ((696) p. 297), *Griffithsia* ((306), (428) p. 653) and other Ceramiaceae ((719) p. 247, (733) p. 132) is followed by outgrowth of the adjacent ones to re-establish continuity. In *Rhodochorton* ((279) p. 203) injury to a filament results in active division of the next intact cell.

Repeated reference has been made in the foregoing pages (pp. 466, 484, 588) to *vegetative reproduction*, which is effected in diverse ways, and it cannot be doubted that in many Red Algae this is a source of

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prolific multiplication (119). Specialised propagules are known only in few Florideae; to the instances described later (see pp. 627, 655) may be added the *Sphacelaria*-like propagules recorded in *Polysiphonia furcellata* Harv. ((65) p. 311).

(e) *Loose-lying Forms*

A considerable number of perennial Florideae (*Polyides*; *Gracilaria*; *Phyllophora* (426) p. 86, (661) pp. 36, 111; *Chondrus* (688) p. 173; *Gigartina*; *Chondria*; *Halopithys*) are capable of surviving after detachment from the substratum (cf. also (5) p. 9). Sernov (610) records the occurrence of *Phyllophora* over an area of about 2000 square miles in the Black Sea. The majority of such loose-lying forms ((558) p. 609, (565) p. 43) occur in seas with a sandy or muddy bottom, like the Baltic (661) and Adriatic (579), where the salt-concentration is low and there is often some pollution. According to Schiller the loose-lying communities of the Adriatic are composed of species that show marked indifference to the composition of the water and are capable of withstanding a considerable range of illumination and temperature.

The loose-lying communities originate from detached individuals which are transported to their destination by currents. Multiplication is effected by vegetative means, since most of the plants are sterile. As a general rule they are richly branched, while the foliose types tend to develop narrow segments. Sometimes they assume a globular aegagropilous form, as in *Furcellaria fastigiata* and *Rytiphloea tinctoria* ((538) p. 26, (558) p. 171, (579) p. 77, (661) p. 130). Such balls are also recorded in *Peyssonnelia polymorpha* ((226) p. 208), as well as in *Lithophyllum* and *Lithothamnion*, cf. *Lithophyllum expansum* f. *stictaeformis* (Aresch.) Foslie ((226) p. 244; *Melobesia agariciformis* Aresch. (276) pl. 73), *L. racemus* (Lam.) Foslie (*Lithothamnion crassum* Phil. (526) p. 243) and *Lithothamnion calcareum* Aresch. ((413); *L. coralloides* Crouan).

B. THE PROCESSES OF REPRODUCTION

1. The General Features of Reproduction

The general course of the life-cycle has already been indicated (p. 413; see also I, p. 51). In the advanced Florideae it exhibits complications which have no parallel in other classes. Most Florideae exhibit sexual reproduction, as was first established by Bornet and Thuret (67), who also gave a clear description of the organs involved; their epoch-making memoir gives a résumé of earlier views (see also (672)). They recognised that the carposporangia, formed as a result of sexual fusion, frequently arose, not from the female organ itself, but from other cells—near at hand or remote—and they commented on the probable importance of these features in classification. Further confirmation was afforded by the work of Janczewski (326) and particularly by that of Schmitz (586), while Oltmanns (499) elucidated certain important

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details of the post-fertilisation changes. The present century has seen progress along a diversity of lines, thanks especially to the many detailed researches of Kylin, Lewis, Phillips and Svedelius.

Many Florideae possess distinct male and female plants, although several Nemalionales and Corallinaceae, for example, are monoecious (cf. (347) p. 236). Not uncommonly the male plants are smaller than the female ((347) p. 231) and they often perish altogether or almost entirely after liberation of the male cells. Their frequent ephemeral nature probably accounts for their rare discovery in diverse Florideae ((676) p. 385). In *Griffithsia* Lewis ((430) p. 241) found groups of four plants with interwoven rhizoids, presumably the products of germination of the four spores of a tetrasporangium; two of these plants were male and two female, implying genotypic sex-determination.

(*a*) *The Female Organs*

The female organ or *carpogonium* ((586) p. 223) consists of a dilated basal portion (fig. 221 A, *cp*; D) harbouring the female cell and a usually narrow, elongate process (*t*), the *trichogyne* ((67) p. 141), which constitutes the receptive organ for the male cells and commonly has a very gelatinous membrane. The female protoplast, which contains some reserves, exhibits no contraction either before or after fertilisation. In most Florideae the cytoplasm of the carpogonium is devoid of chromatophores, but in certain Nemalionales (*Acrochaetium*, *Nemalion*, *Batrachospermum*, etc.) these are present in the basal part and may even extend far into the trichogyne ((177) p. 446, (506) p. 110). The cytoplasm of the latter generally contains a nucleus (fig. 221 C–E, *tn*; cf. (347) p. 210), which is a sister of the female one (*f*). A trichogyne nucleus has not always been found (cf. e.g. (380) pp. 27, 118), but its absence is difficult to prove conclusively since it usually degenerates at an early stage. It is probably a vestigial structure.

In most Florideae the carpogonium terminates a short, often 3-4-celled, lateral ((387) p. 107), spoken of as the *carpogonial branch* (figs. 221 A–C; 223 N, *cb*); the cell (*su*) from which this branch arises is termed the *supporting cell* ("Tragzelle"). In forms with a compact thallus the carpogonial branch usually arises from an internal cell (fig. 221 B), and it is the function of the trichogyne (*t*) to maintain connection with the external medium. Such carpogonial branches, however, often (e.g. *Cystoclonium*) arise near the growing tips from cells situated close to the surface, although as growth progresses the supporting cell becomes deeply embedded. In the less specialised forms the lower cells of the carpogonial branch often bear laterals (fig. 239 A, *l*), but these are lacking in Rhodymeniales, Ceramiales, and most Gigartinales. In some members of these orders the cells of the carpogonial branch contain several nuclei (figs. 223 N; 254 A, *n*), and this may indicate arrested branch-formation ((389) p. 75). In

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diverse Nemalionales the carpogonial branches are part of the normal branch-system, but in most Red Algae they constitute accessory laterals ((39) p. 10). The cells of the carpogonial branches are commonly colourless.

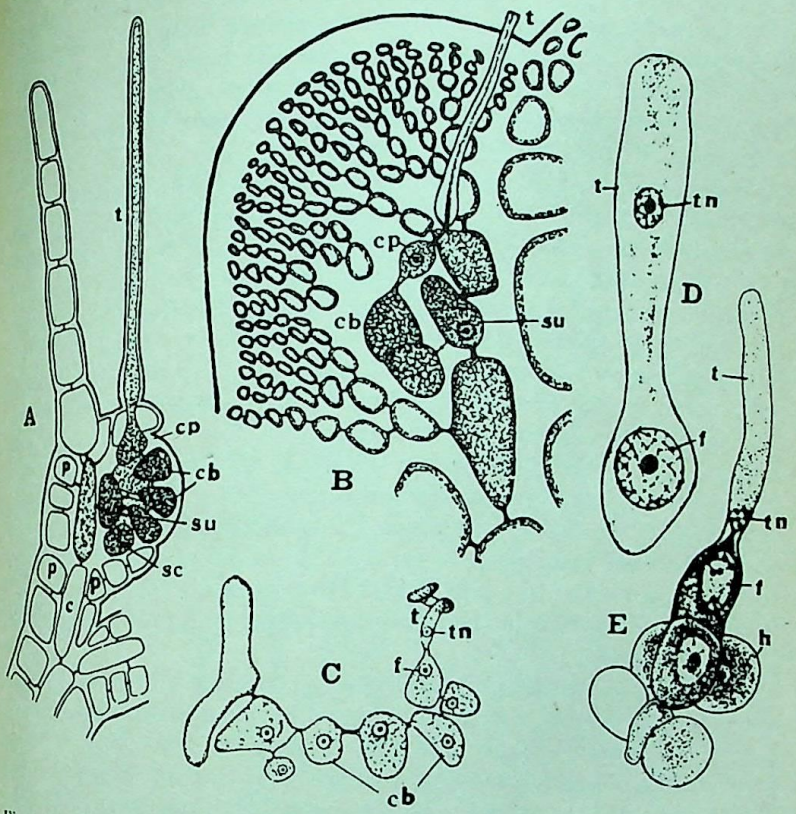

Fig. 221. Carpogonia of Florideae. A, *Rhodomela virgata* Kjellm. B, *Plocamium coccineum* (Huds.) Lyngb. C, *Dumontia incrassata* Lamour. D, *Polysiphonia violacea* (Roth) Grev. E, *Scinaia furcellata* (Turn.) Bivona. *c*, axial cell; *cb*, carpogonial branch; *cp*, carpogonium; *f*, nucleus of female cell; *h*, hypogynous cells; *p*, pericentrals; *sc*, sterile cell; *su*, supporting cell; *t*, trichogyne; *tn*, trichogyne nucleus. (D after Yamanouchi; E after Svedelius; the rest after Kylin.)

(*b*) *The Male Organs*

The antheridia of Florideae ((5) p. 78, (258), (259) p. 175, (586) p. 222, (663) p. 71, (667), (756) p. 409) are spherical or oblong, unicellular structures, producing a single male cell or *spermatium* ((246) p. 80) from the entire contents. As a rule they arise in large numbers in close proximity to one another (fig. 222 B, *a*) so as to form white or

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pale-coloured dots or patches (sori), visible to the naked eye.[1] Several antheridia (figs. 222 D, *1–4*; 257 D), often 3, sometimes 2, 4, or 5, are produced successively from a common mother-cell (*m*) which is often elongate (fig. 222 H, J, *m*). The mother-cells, which usually (⟨258⟩ p. 241) terminate short, often densely compacted, branch-systems (fig. 222 A, B, J) and are invariably uninucleate, commonly possess reduced chromatophores and are sometimes altogether colourless (⟨663⟩ p. 62). They often form a palisade-like layer, especially in the more compact types. In a few of the more primitive Florideae (e.g. *Batrachospermum*, fig. 227 D) the mother-cells are not differentiated from the vegetative cells.

As a general rule (fig. 222 E) the antheridia (*a*) first appear as protuberances, which usually arise subterminally (fig. 222 J, *a*) and successively (fig. 222 D, *1–4*) from different sides of the mother-cell (*m*). As an antheridial protuberance develops, the nucleus shifts to the point of origin and enters into early prophase (fig. 222 F). After completion of mitosis one daughter-nucleus enters the antheridium (fig. 222 E, *a*), while the other again passes to the base of the mother-cell; there is difference of opinion whether the latter enters into a resting condition before it divides again, and this is perhaps a variable feature. The antheridium is cut off by an oblique annular ingrowth of the wall (fig. 222 G). In *Martensia* (⟨663⟩ p. 64) and in certain other instances (cf. fig. 238 C), in which the antheridia (*an*) arise terminally and sometimes form short rows, the septum is transverse. Where, as in *Chondrus crispus* (fig. 222 J) and *Furcellaria fastigiata* (fig. 222 K), there is a thick cuticle (*cu*), the developing antheridia successively pierce the latter.

The mature antheridium commonly possesses a thick wall which, according to Grubb (⟨258⟩ p. 243), sometimes consists of three distinct layers—a narrow deeply staining outermost one, an intervening gelatinous layer which swells considerably at the time of spermatium-liberation, and a narrow, highly refractive innermost one. The nucleus is large (fig. 222 H, I), while the scanty cytoplasm is usually quite colourless, although in *Batrachospermum* (⟨165⟩ p. 56, ⟨506⟩ p. 111, ⟨582⟩ p. 128) and *Nemalion* (⟨136⟩ p. 333) it includes remains of chromatophores, at least in early stages. The spermatium is liberated through a narrow apical split in the elastic wall (fig. 222 C). Several investigators (e.g. ⟨605⟩ p. 239, ⟨756⟩ p. 410) report that the spermatium

[1] Diverse earlier workers (Thuret, Buffham) speak of such aggregates as antheridia and of the individual male organs as spermatangia (cf. ⟨192⟩ p. 93), and the latter designation is retained by many recent writers (Svedelius, Kylin). It is certainly unwarranted to describe the whole complex of male organs by the name antheridium, while despite the reasons that have been urged for using the term spermatangium (cf. e.g. ⟨663⟩ p. 77), I agree with Oltmanns (⟨502⟩ p. 361) that there is no case for a double terminology and that, as in other classes of Algae, the structure producing the male cells should be designated antheridium.

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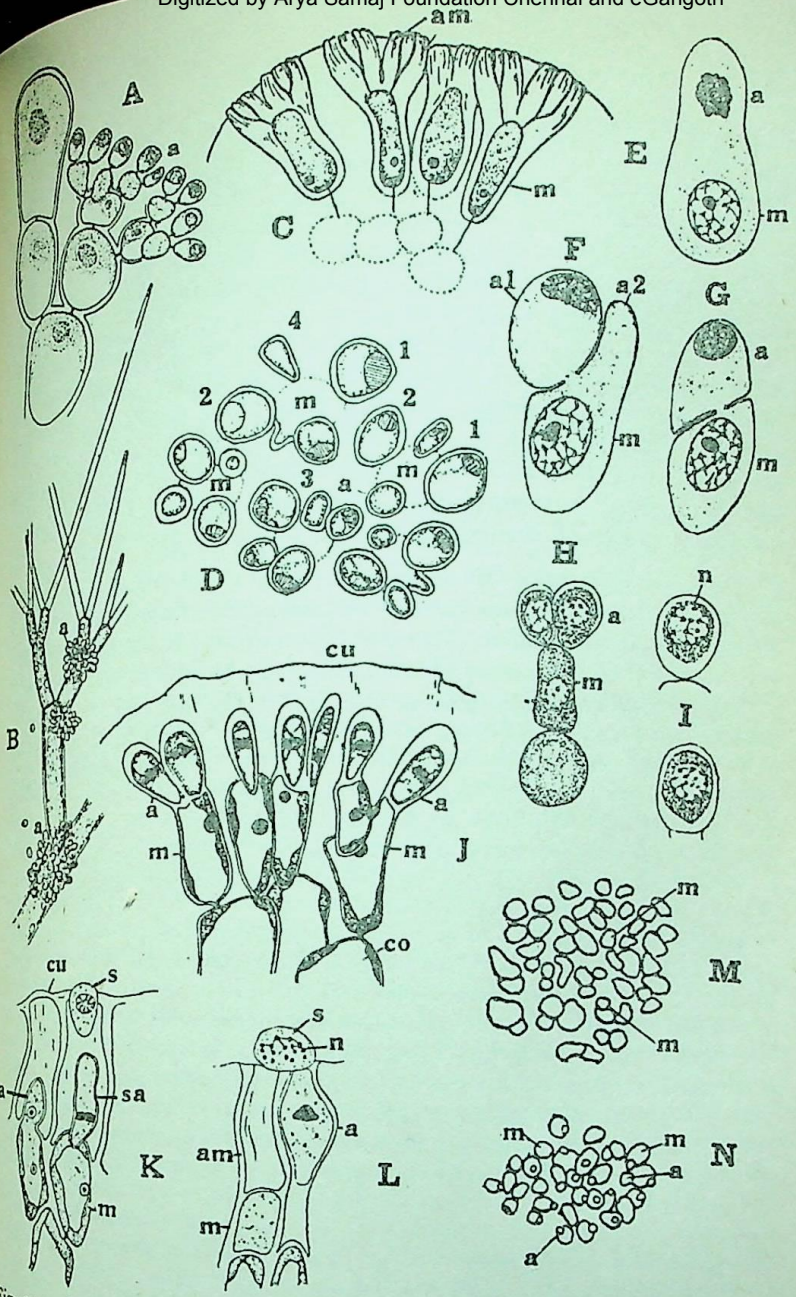

Fig. 222. Antheridia and antheridial development in Florideae. A, *Helminthocladia Calvadosii* (Lamour.) Setch. B, *Callithamnion corymbosum* (Smith) C. Ag. C–G, *Polysiphonia violacea* (Roth) Grev.; D seen from the surface; E–G, stages in formation of antheridia. H, I, *Bonnemaisonia asparagoides* (Woodw.) Ag. J, *Chondrus crispus* (L.) Stackh. K, L, *Furcellaria fastigiata* (Huds.) Lamour. M, N, *Ceramium rubrum* (Huds.) C. Ag., seen from the surface. *a*, antheridia; *am*, antheridial wall; *co*, cortex; *cu*, cuticle; *m*, mother-cell; *n*, nucleus; *s*, spermatia; *sa*, secondary antheridia. The numerals in D and F indicate the order of development of the antheridia. (A after Kylin; B after Thuret & Bornet; E–G after Yamanouchi; H, I after Svedelius; the rest after Grubb.)

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is constituted by the entire detached antheridium, but various statements of this kind have subsequently been disproved ((258) p. 214) and all are suspect; in the Corallinaceae (p. 649), however, there is at present no evidence of dehiscence of the antheridia. After production of the primary antheridia, the same mother-cell may form a secondary series (figs. 222 K; 242 G, *sa*) by proliferation into the empty membranes of the first-formed ones.

The nucleus of the free spermatium seems invariably to be in prophase (fig. 222 I, L), without an evident nuclear membrane and with a number of deeply staining chromatin granules united by delicate threads. That of the mature antheridium is also often in prophase, but there is considerable evidence that prior to this it has passed through a resting stage. The male nucleus remains in the prophase condition during its passage down the trichogyne.

There is difference of opinion as to the presence (Falkenberg, Guignard, Grubb, Yamanouchi) or absence (Kylin, Schmitz, Svedelius)[1] of a membrane around the liberated spermatium, although it is generally agreed that there is a delicate membrane in later stages, especially in spermatia adhering to trichogynes. Grubb ((258) p. 244; cf. also (259)) states that in certain species (e.g. *Polysiphonia fastigiata*) a membrane is recognisable around the spermatium before dehiscence of the antheridium. The question is undecided, but the capacity for slight amoeboid change of shape exhibited by the spermatia of certain Florideae does not speak for the universal presence of a membrane.

Svedelius ((674) p. 227; cf. also (347) p. 210), emphasising the resemblance between an antheridial mother-cell after nuclear division has occurred (fig. 222 E) and a young carpogonium with its trichogyne (fig. 221 D), regards these two parts of the female organ as respectively homologous with the mother-cell and the antheridium. The frequent presence of a constriction, accompanied by thickening of the wall, at the base of the trichogyne (cf. e.g. fig. 227 G), is regarded as indicating a former division into two cells. Schussnig ((604) p. 542, (605) p. 254, (606) p. 242) and Kylin ((389) p. 74), on the other hand, regard the entire carpogonium as homologous with an antheridium. This view is based on the occasional division of the antheridial nucleus (cf. below), while the usual prophase condition of the spermatium-nucleus is taken as indicative of a former division (cf. (258) p. 247). In *Spermothamnion hermaphroditum* replacement of the terminal cell of the procarp by an antheridium has been recorded ((326) p. 117).

(c) *Fertilisation*

The spermatia probably often have approximately the same specific gravity as the surrounding medium so that they remain floating for some considerable time. Their large numbers ensure contact with a trichogyne, the tip of which is evidently more or less mucilaginous.

[1] See (365) p. 321, (371) p. 57, (375) p. 114, (376) p. 552, (380) p. 105, (588) p. 222, (594) p. 231, (667) p. 256.

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In *Phyllophora membranifolia* ((562) p. 78) the spermatia perform slow gliding movements, similar to those reported for the carpospores and tetraspores of certain Florideae, and these are perhaps of wider occurrence. They will facilitate contact with trichogynes that do not project markedly or are embedded in mucilage (cf. also (586) p. 222). At the point of contact both the membrane of the spermatium and the wall of the trichogyne are dissolved (fig. 223 A, B), leaving an open passage for the nucleus of the male gamete. In later stages the spermatium-membrane appears empty (fig. 223 D, *s*), but the fate of the male cytoplasm is uncertain. In *Batrachospermum* the emission of definite copulating processes by the spermatia has been recorded ((165) pp. 57, 65, (582) p. 128).

In *Batrachospermum* ((378) p. 158, (582) p. 128) and *Nemalion* ((136) p. 334, (377) p. 261, (748) p. 617) the spermatium-nucleus ordinarily divides after contact with the trichogyne, although only one nucleus fuses with the female. Among the more specialised Florideae no such division takes place[1] and its occurrence in these relatively primitive types suggests that the antheridium of Florideae may be derived from an organ producing more than one gamete (cf. p. 596); traces of division perhaps persist in the invariable prophase condition of the spermatial nucleus.

Wille (746) first described in *Nemalion* the passage of the male nucleus to the basal part of the carpogonium (cf. fig. 233 B), the apposition of the two sex nuclei (fig. 223 A, H, *n*), and their fusion. The last process (fig. 223 F, G) has not often been observed ((42) p. 12, (378) p. 158, (506) p. 111, (756) p. 415, (757) p. 95), but indirect evidence of the production of a diploid fusion nucleus is considerable, and in a large proportion of Florideae fertilisation no doubt follows on contact of a spermatium with a trichogyne. As the male nucleus advances, the cytoplasm of the trichogyne not uncommonly shows signs of disorganisation, exhibiting numerous particles staining deeply with haematoxylin, whilst the part in front is still homogeneous (cf. (680) p. 34). The female nucleus seems frequently to move a short distance upwards to meet the male ((499) p. 102, (746), (756) p. 415).

At the moment of fusion (fig. 223 F) the male nucleus (*m*), in *Polysiphonia* ((756) p. 415), consists of a dense aggregate of chromosomes, while the female (*f*) is in a resting condition (cf. also fig. 223 N and (668) fig. 16). In *Batrachospermum* ((378) p. 158) and *Nemalion* ((377) p. 266), on the other hand, both nuclei are in a resting condition. In *Polysiphonia* the membrane of the female nucleus dissolves at the point adjacent to the male chromosomes (fig. 223 G), after which chromosomes differentiate in the female nucleus and the two sets mingle with

[1] Spermatia with two nuclei have been reported in species of *Lithophyllum* ((558) p. 267), while Suneson (659) states that those of Corallinaceae exhibit later stages of nuclear division than are usual in other Florideae.

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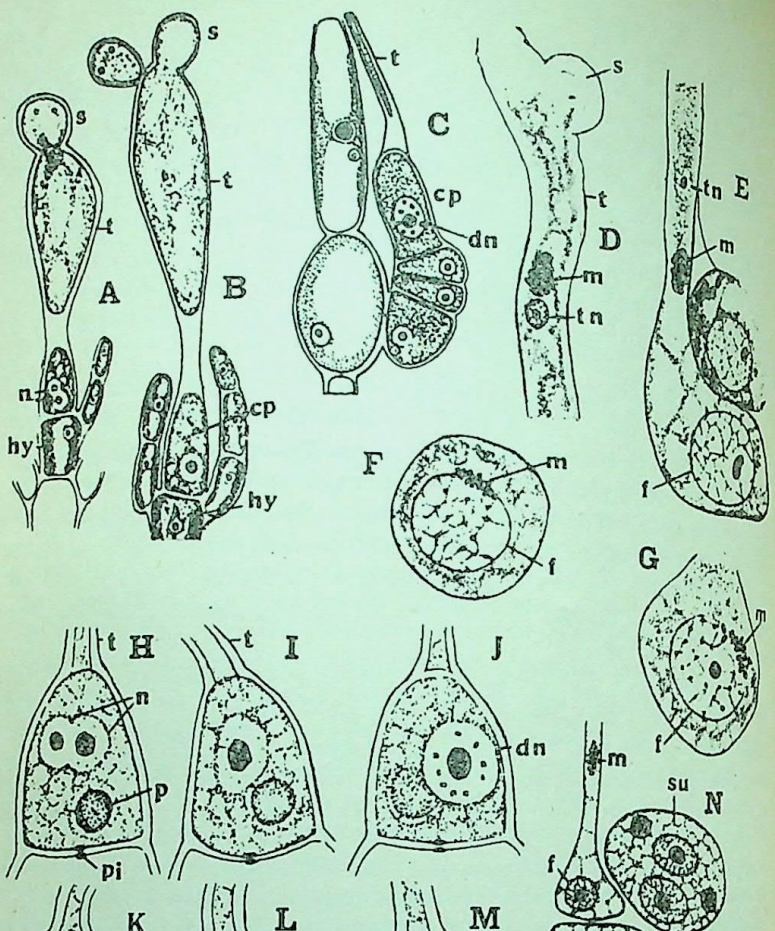

Fig. 223. Fertilisation in Florideae. A, B, *Batrachospermum moniliforme* Roth, post-fertilisation stages. C, *Helminthora divaricata* J. Ag., post-fertilisation. D–G, *Polysiphonia violacea* (Roth) Grev., successive stages in passage of male nucleus and nuclear fusion. H–M, *Nemalion multifidum* (Web. & Mohr) J. Ag., nuclear fusion and meiosis. N, *Griffithsia corallina* (Lightf.) Ag., passage of male to female nucleus. *cb*, carpogonial branch; *cp*, carpogonium; *dn*, diploid nucleus; *f*, female nucleus; *hy*, hypogynous cell; *m*, male nucleus; *p*, pyrenoid; *pi*, pit-connection; *s*, spermatium; *su*, supporting cell; *t*, trichogyne; *tn*, trichogyne nucleus. (D–G after Yamanouchi; the rest after Kylin.)

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one another. The fusion nucleus then passes into prophase, its membrane disappears, and division commences.

After penetration of the male nucleus the trichogyne becomes separated at its base from the rest of the carpogonium (fig. 223 A–C); this is commonly effected by progressive thickening of the membrane until complete closure occurs, although sometimes the channel seems to be blocked by a plug of membrane-substance ((599) p. 302). The trichogyne either persists for some time or rapidly withers. In *Nemalion* ((136) p. 337, (748) p. 618; cf. also (377) p. 261) the zygote is stated to become surrounded by a distinct membrane which serves to cut off the trichogyne, although the pit-connection with the hypogynous cell is maintained.

(*d*) *Post-fertilisation Changes and the general Features of the Life-cycle*

In Nemalionales the first nuclear divisions within the fertilised carpogonium are meiotic (fig. 223 C, J, *dn*), but in most Florideae they are mitotic, reduction being postponed to the time of tetraspore-formation. The fertilised carpogonium invariably puts forth one or more threads (fig. 227 H, *g*), the ultimate function of which is the production of asexual spores (*carpospores*), but the manner of formation of the latter varies in the different orders. In Nemalionales the haploid threads or *gonimoblasts* ((599) p. 303), arising from the carpogonium, produce the carpospores directly (figs. 227 K; 230 E, *g*). The threads in question are for the most part relatively short and well branched so as to form a dense cluster, and certain enlarged cells (often terminal), filled with cytoplasm and food-reserves, constitute *carposporangia* (*ca*), from each of which a single naked carpospore is liberated. The latter gives rise to a plant which again bears sex organs so that in the life-cycle of Nemalionales the zygote constitutes the only diploid stage, while there are two haploid phases, the ordinary seaweed and the gonimoblast-threads originating from the zygote (cf. *Coleochaete*). Such Florideae have been designated *haplobiontic* by Svedelius ((671) p. 42; cf. also (511)).[1] In several Nemalionales the sexual phase also bears sporangia forming accessory spores (1, p. 51), mostly monospores (p. 623).

In the remaining Florideae the threads, arising from the fertilised carpogonium, contain diploid nuclei and are formed singly or in small numbers (fig. 224 A, G, *co*). They grow towards and establish contact with certain cells (*a*),[2] which are situated near at hand or at a more or less considerable distance and are often specially differentiated by size or rich contents; in certain orders these *auxiliary cells* ((586) p. 229) are clearly recognisable before the threads from the carpo-

[1] Regarding the frequent incorrect use of this term, see (678) p. 39.
[2] The Gelidiales show special features (see p. 628).

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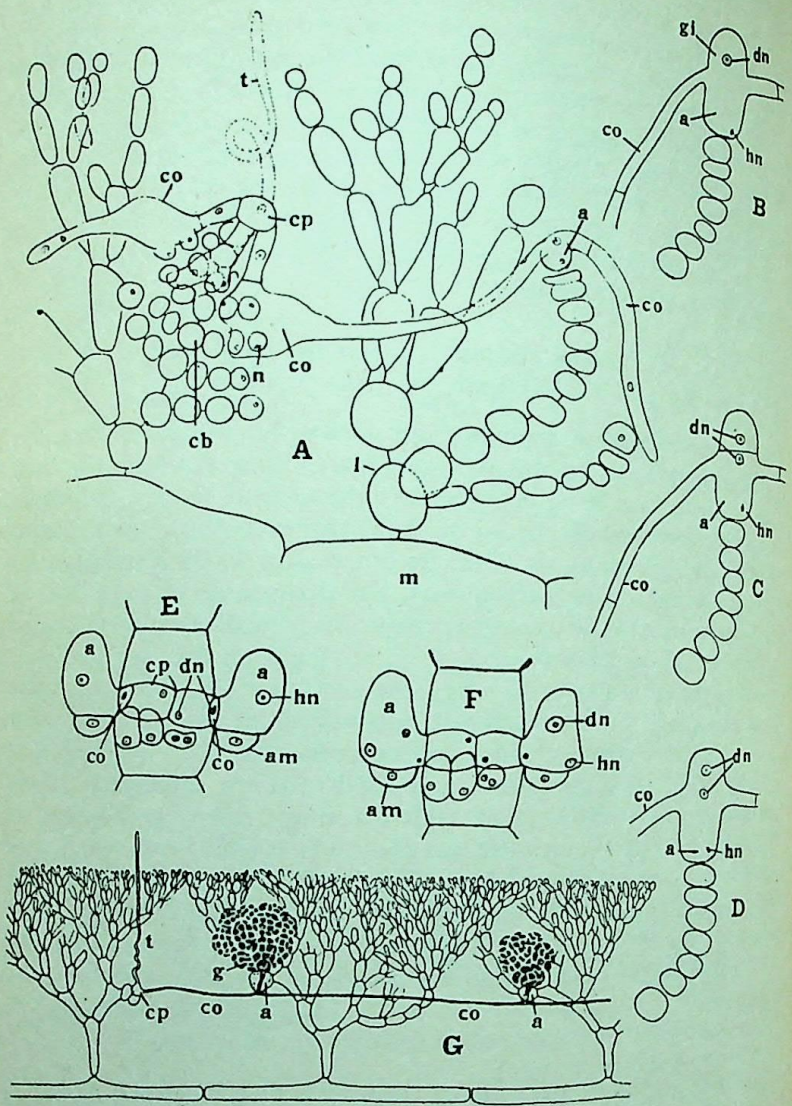

Fig. 224. Post-fertilisation changes in diplobiontic Florideae (diagrammatic). A–D, *Acrosymphytum purpuriferum* (J. Ag.) Kyl. E, F, *Callithamnion corymbosum* (Smith) C. Ag. G, *Platoma Bairdii* (Farl.) Kuck. *a*, auxiliary cell; *am*, auxiliary mother-cell; *cb*, carpogonial branch; *co*, connecting filament or cell; *cp*, carpogonium; *dn*, diploid nucleus; *g*, gonimoblast; *gi*, gonimoblast initial; *hn*, haploid (auxiliary cell) nucleus; *l*, lateral; *m*, axial cell; *n*, nutritive cell; *t*, trichogyne. (G after Kuckuck; the rest after Oltmanns.)

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gonia reach them. When auxiliary cells and carpogonia form parts of the same branch-system (figs. 237 F; 256 B), the aggregate is spoken of as a *procarp*. The threads that establish contact with the auxiliary cells are spoken of as *connecting filaments*[1] ("Verbindungsfäden" of Berthold ((39) p. 10), a term that is specially appropriate in diverse Cryptonemiales (*Acrosymphytum*, fig. 224 A) and Gigartinales (*Platoma*, fig. 224 G), in which the auxiliary cells (*a*) are widely separated from the carpogonia (*cp*) so that the connecting filaments (*co*) are of considerable length. In the more specialised Florideae (e.g. Ceramiales), however, the connecting filaments are extremely short, being represented merely by a small cell (fig. 224 E, *co*).

At the point of contact (fig. 224 B, left-hand side of E) the membranes dissolve and communication is established between the cell of the connecting filament (*co*) and the auxiliary cell (*a*). Oltmanns (499) showed that this fusion is purely cytoplasmic and that the nuclei of connecting cell (diploid, *dn*) and auxiliary cell (haploid, *hn*) not only fail to fuse, but usually remain far apart. The fusion with the auxiliary cell, however, affords a stimulus, since division of the nucleus of the connecting cell (fig. 224 D, *dn*; also often of the auxiliary cell, cf. (499) p. 107) ensues, and it is at these points that gonimoblast-filaments (fig. 224 G, *g*) arise and that carpospores are produced.[2] Among the less specialised types the same connecting filament may fuse successively with a number of auxiliary cells (fig. 224 A, G) resulting in several centres of carpospore-formation, but in the higher Florideae there is fusion with only one auxiliary cell and, since there is often but a single connecting filament, only one group of gonimoblasts results from the act of sexual fusion.

In a few instances (cf. fig. 224 C and p. 641) the gonimoblasts arise from the connecting filament, but mostly the two diploid nuclei of the latter actually pass into the auxiliary cell (fig. 224 F). While its nucleus (*hn*) and one of the nuclei from the connecting cell disorganise, it is from the auxiliary cell itself with the other diploid (foreign) nucleus that the gonimoblasts are produced. One can speak here of a carposporophyte ((133) p. 331), but, since the gonimoblasts of these forms are obviously homologous with the haploid ones of Nemalionales, the term is not a generally useful one.

The auxiliary cells ((398) p. 141) are sometimes modified cells of a lateral branch-system composing the thallus (e.g. *Platoma*, fig. 224 G, *a*), but more usually they are, like the carpogonia, situated on accessory branches (*Acrosymphytum*, fig. 224 A). Although commonly dif-

[1] At one time also called ooblastema filaments. Oltmanns ((499) p. 102, (502) p. 386) speaks of them as sporogenous threads, a term also used by Kylin in his earlier papers.

[2] In certain Florideae the connecting filaments first fuse with cells resembling auxiliary cells, but these *nutritive cells* (fig. 224 A, *n*) do not provide a stimulus for carpospore-formation (cf. p. 635). Comparable phenomena occur in some Nemalionales (p. 614).

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ferentiated already prior to fertilisation, in many Rhodymeniales (fig. 267 A) they remain inconspicuous until sexual fusion has occurred, while in Ceramiales (figs. 270 A; 273 A) their formation is deferred until after fertilisation. In these orders the auxiliary cells are closely associated with the carpogonial branch. The nature of the auxiliary cells is disputed; while Kylin ((389) p. 75) looks upon them as modified vegetative cells, Schussnig ((604) p. 544, (605) p. 246) regards them as homologous with rudimentary carpogonial branches.

In all Florideae, except Nemalionales, the carpospores are of course diploid, although they are produced from the gonimoblasts in essentially the same way as in haplobiontic forms. The carpospores give rise to a diploid plant, which usually resembles the haploid one in all respects, except that it normally bears only asexual sporangia forming four spores (*tetrasporangia*, fig. 225). The two nuclear divisions in the sporangium are meiotic and the tetraspores grow into sexual individuals. The life-cycle of these Florideae therefore includes a haploid sexual and two diploid asexual phases (the gonimoblasts producing carpospores, the tetrasporic plant) and such Florideae are described as *diplobiontic* by Svedelius ((671) p. 43). There are three successive generations, although there is only one alternation of cytological phases in the life-cycle (83). The isomorphic alternation between the sexual and the tetrasporic individuals was first demonstrated experimentally by Lewis (430, 431). He allowed the two kinds of spores to germinate on oyster-shells which, with the germlings, were transferred to the open sea, the tetraspores growing into mature sexual plants and the carpospores into asexual ones. The relation between the diplobiontic and haplobiontic types of life-cycle is discussed on p. 736.

The naked carpospores sometimes perform gliding movements ((129) p. 224, (154) p. 1047, (562) p. 76), while amoeboid changes of shape ((67) p. 143, (111), (120), (129) p. 222, (363) p. 194, (692) p. 64), not necessarily associated with movement, have been reported by various observers. It is not known whether such movements aid in the adoption of a suitable substratum. Proliferation of carposporangia (fig. 227 E) occasionally occurs ((586) p. 228). Chemin ((129) p. 220) gives data on the mode of liberation of these spores.

(*e*) *Tetrasporangia and Tetraspores*

The tetrasporangia ((5) p. 88) of the diplobiontic Florideae are enlarged cells, which possess dense cytoplasmic contents and are almost invariably terminal on short lateral branches. This is clearly evident in such loosely branched forms as *Callithamnion* (fig. 225 A, *t*) and *Antithamnion* (fig. 289 A), but even in genera with a compact structure (e.g. *Chondrus*, fig. 263 I; *Dumontia*, fig. 225 F, *t*), where they are embedded in the superficial tissues, their terminal position is generally recognisable without difficulty. The four spores either

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form a row (*zonate*) as in many Cryptonemiales and Gigartinales (fig. 225 B, *t*), or they are arranged crosswise (*cruciate*), commonly in the same plane, as for example in Rhodymeniales (fig. 225 E, *t*), or lastly they are grouped in a tetrad (*tetrahedral*) as in the majority of

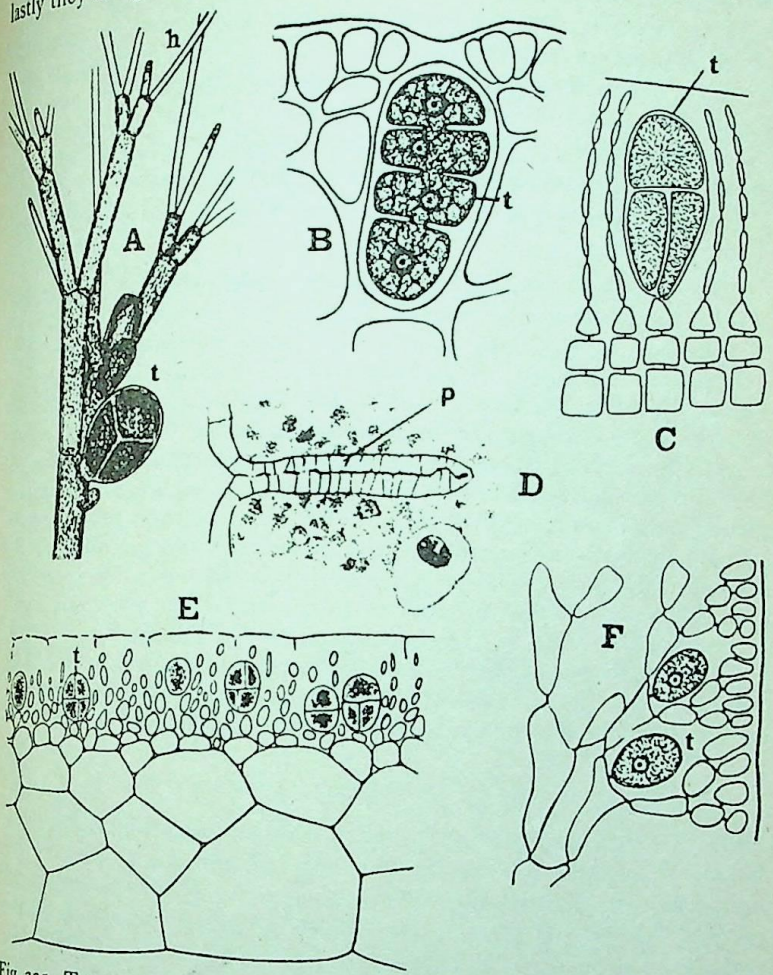

Fig. 225. Tetrasporangia of Florideae. A, *Callithamnion corymbosum* (Smith) C. Ag. (tetrahedral). B, *Cystoclonium purpureum* (Huds.) Batt. (zonate). C, *Peyssonnelia Dubyi* Crouan (cruciate). D, *Delesseria sanguinea* Lamour., septum-formation in tetrasporangium. E, *Chrysimenia ventricosa* (Lamour.) J. Ag. (cruciate). F, *Dumontia incrassata* Lamour., development of sporangia. *h*, hair; *p*, plasmodesmae; *t*, tetrasporangium. (A after Thuret & Bornet; D after Svedelius; E after Kuckuck; the rest after Kylin.)

the Ceramiales (fig. 225 A, *t*). Different types may occur in different species of the same genus ((347) p. 216) and occasional transitions are found. Certain Florideae, especially Corallinaceae, produce only two spores (*bispores*) in the sporangia (cf. pp. 655, 731).

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The mature sporangia are usually uninucleate,[1] even when the vegetative cells contain several nuclei (cf. however p. 716). Except in the cruciate type, the two nuclear divisions usually precede any cleavage of the cytoplasm. After the four nuclei have assumed their definite position, the cytoplasm exhibits peripheral invaginations which, advancing centripetally (fig. 225 B), divide the protoplast into as many uninucleate portions. The young sporangia are vacuolate ((356) p. 985) and the chromatophores are often indistinct even in the mature spores. The liberated tetraspores are always naked and gliding movements, similar to those of the carpospores, are reported ((558) p. 329, (562) p. 75), while Chemin ((129) p. 222) records amoeboid changes of shape.

Cleavage of the protoplast is commonly accompanied by the ingrowth of septa from the wall of the sporangium ((35) p. 374, (453) p. 14, (502) p. 358, (665) p. 302, (735) p. 162), but little detailed information is available on this point. In *Delesseria* (fig. 225 D) the gelatinous septa show a cellulose-reaction and, like the wall of the sporangium, are traversed by pores occupied by plasmodesmae (*p*). In the formation of cruciate tetraspores transverse division of the contents ensues after the first nuclear division, the two halves then dividing longitudinally, the planes of division coinciding or not (fig. 225 C, E); septum-formation seems commonly to accompany the division of the protoplast in this instance, but it is not clear whether this is the rule. There are few available data (cf. (129) p. 219) as to the mode of dehiscence of the sporangia; according to Westbrook ((739) p. 67) those of *Callithamnion* (cf. fig. 294 K) open by a lid, those of some species of *Antithamnion* by an apical split. Proliferation of tetrasporangia is probably not infrequent, especially in the less specialised forms ((363) p. 191, (735) p. 162).

(*f*) *The Reduction Division*

Despite a few exceptions (p. 725), the tetrasporangium of diplobiontic Florideae is usually the seat of meiosis. This was first established by Yamanouchi in *Polysiphonia* (755), who thus confirmed certain suggestions made earlier ((501) p. 273). Since then meiosis has been demonstrated in the tetrasporangia of a considerable number of diplobiontic Florideae, but there are considerable discrepancies as regards the details of the process, in part centring about the question as to the relation between nucleolus and chromatin (p. 413).

The tetrasporangium nucleus, which enlarges appreciably before meiosis commences, shows a conspicuous network with chromatin granules at the corners and a large prominent nucleolus (fig. 226 A, B, L). In *Polysiphonia* ((756) p. 420) the spireme formed during prophase affords evidence of a double nature (fig. 226 C). This is more distinct when the thread again spreads through the nuclear cavity (fig. 226 F), after the rather prolonged synezesis (fig. 226 E). Subse-

[1] The peculiar views of Heydrich (298) cannot be discussed.

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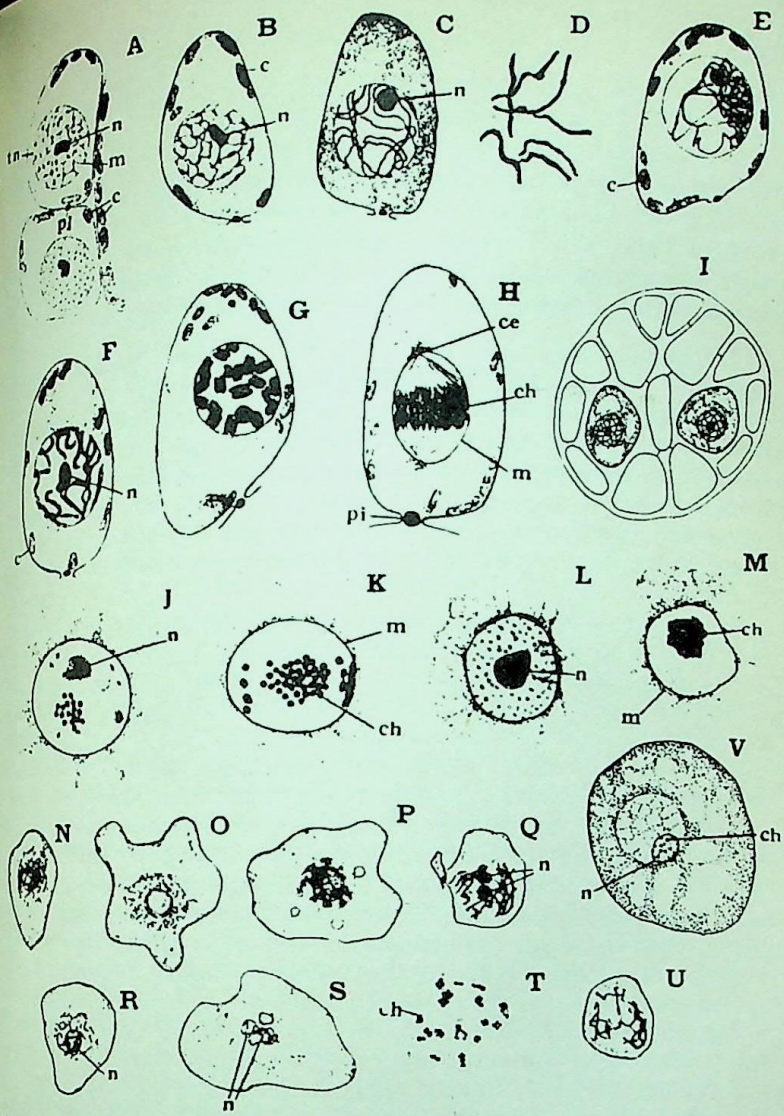

Fig. 226. Meiosis in the tetrasporangium. A–H, J, K, *Polysiphonia violacea* (Roth) Grev. (after Yamanouchi); A, mother-cell nucleus with delicate network; B, network coarser; C, parallel arrangement of chromatin threads; D, some of the latter; E, synezesis; F, nucleus emerging from synezesis; G, late prophase, diakinesis; H, metaphase; J, polar view of first mitosis in germinating tetraspore (20 chromosomes); K, ditto of first mitosis in carpospore (40 chromosomes). I, *Rhodomela virgata* Kjellm. (after Kylin), transverse section showing two sporangial initials, nuclei in spireme stage. L, M, *Delesseria sanguinea* Lamour. (after Svedelius); L, nucleus of mother-cell in prophase; M, synezesis. N–P, *Rhodomela subfusca* (Woodw.) Ag. (after Westbrook); N, O, diminution of chromatin; P, diakinesis. Q–T, *Laurencia hybrida* (Decsne) Ag. (after Westbrook), prophase stages; Q, spireme stage, two nucleoli; R, diminution of chromatin; S, resting stage with several nucleoli; T, diakinesis. U, *L. pinnatifida* (Gmel.) Lamour. (after Westbrook), spireme stage. V, *Lomentaria rosea* (Harv.) Thur. (after Svedelius). *c*, chromatophores; *ce*, centrosome; *ch*, chromosomes; *m*, nuclear membrane; *n*, nucleolus; *pi*, pit-connection; *tn*, tetrasporangium-nucleus.

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quently there is formation of 20 pairs of chromosomes, which gradually shorten to form as many gemini, giving a typical diakinesis-stage (fig. 226 G). By this time the nucleolus has disappeared. The spindles are intranuclear (fig. 226 H), with a centrosome (*ce*) at each pole (cf. also (166)); those of the second division, which are orientated perpendicular to one another, appear as soon as the chromosomes begin to separate. In the telophase of the second division the original nuclear cavity is cut across by the cytoplasmic cleavage.

The course of events is essentially the same in *Rhodomela virgata* (fig. 226 I; (371) p. 62), *Nitophyllum punctatum* (fig. 293 B; (669) p. 51), *Griffithsia corallina* ((375) p. 117, (735) p. 165), *Spermothamnion Turneri* ((176) p. 555) and *Rhodymenia palmata* ((735) p. 159), except that in the first three synezesis was not observed and the spindles are not intranuclear, while in the last two no achromatic figure was seen. Centrosomes were not found in *Spermothamnion* and *Griffithsia*. In the later stages of the heterotype division the bivalents are always short (fig. 226 P, T).

A spireme stage has been reported in many other Florideae,[1] but not in *Delesseria sanguinea* ((665) p. 286), *Griffithsia globifera* ((428) p. 665), *Lomentaria clavellosa* ((680) p. 23), *Corallina*, or *Stenogramma interrupta*. In the last three this has been correlated with the small size and scanty chromatin content of the nucleus ((740) p. 573, (757) p. 92). Westbrook (735, 740), using Feulgen's nuclear stain, concludes that the chromosomes always differentiate from the reticulum and that they exhibit no relation to the nucleolus. Svedelius, on the other hand, records an aggregation of chromatin around the nucleolus at a certain stage in *Delesseria* (fig. 226 M), a condition attributed by Kylin ((380) p. 107; see also (740) p. 576) to imperfect fixation. The former concludes that there is actual penetration and has more recently ((680) p. 13) given a circumstantial account of similar events in the (mitotic) nuclear divisions in the sporangium of *Lomentaria rosea* (fig. 226 V), although no such phenomena are recorded during meiosis in *L. clavellosa*.[2] In *Brongniartella* and certain other Ceramiales peculiar conditions have been reported ((151) p. 29, (515) p. 3, (605) p. 244), suggesting a possible passage of chromatin into the nucleolus during the late prophase, as has recently been affirmed by Geitler[3] also for mitosis in *Spirogyra*. The evidence in all these instances is inconclusive and further investigation is requisite.

In diverse Ceramiales (*Ceramium*, *Chondria*, etc.) the nucleolus fragments into a number of irregular bodies during prophase (fig. 226 Q, S). According to Westbrook several species (especially *Nitophyllum punctatum*) show a diminution of chromatin in the outer nucleus (fig. 226 N, O, R) prior to diakinesis. At this stage ((375) p. 119, (428) p. 665,

[1] Cf. the recent papers of Westbrook (735, 740) and especially the synopsis on p. 169 of the first paper.

[2] Lewis' data (cf. also (605) p. 249) as to the origin of chromosomes by fragmentation of the nucleolus in *Griffithsia* are unsatisfactory ((371) p. 64).

[3] Cf. Geitler, *Ber. Deutsch. Bot. Ges.* **53**, 270–5, 1935.

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(605) p. 244, (665) p. 296, (740) p. 579) the cytoplasm of the sporangial initial often contains granules staining readily with basic dyes and with haematoxylin. Their exact nature remains undetermined, some regarding them as extrusions from the nucleus, while Svedelius and Kylin consider them to arise spontaneously in the cytoplasm. The scanty data on the details of meiosis in the Nemalionales ((136) p. 338, (377) p. 267, (378) p. 161, (671) p. 32, (679) pp. 27, 46) indicate the customary succession of spireme, synezesis, and diakinesis, although in most instances only the last-named stage has been observed.

The haploid number of chromosomes ((347) p. 216, (679) p. 55) appears to approximate to 10 in most haplobiontic Florideae, although the number is 20 in *Bonnemaisonia asparagoides* ((376) p. 556, (679)) and this is also that usually reported in the diplobiontic forms (cf. (735) p. 169).

(g) *The early Stages of Germination*

Tetraspores and carpospores are nearly always heavier than water and tend to sink. The secretion of a membrane is possibly the result of contact with a substratum (379), whilst attachment is in all probability due to the production of mucilage. The mature spores are nearly always filled with starch. The contents are deeply pigmented, but the chromatophores are difficult to distinguish and perhaps not fully differentiated ((129) p. 218). During the early stages of germination, as the reserves disappear, the chromatophores become apparent (339). There is no resting period. There are usually no essential differences in the germination of carpospores and tetraspores ((173) p. 247, (428) p. 673, (558) p. 504), although some difference in size of the germlings has occasionally been reported ((339) p. 249).

The plane of the first division-wall is not determined by the direction of the incident light ((339) p. 237, (379) p. 22, (483) p. 185, (552) p. 128), although Tobler ((699) p. 150), without apparent evidence, supposes that this is so in *Griffithsia opuntioides*. Kylin suggests that there may be an influence of the substratum or perhaps of gravity (cf. however (37) p. 572). According to Chemin ((126), (129) p. 510) the spores of many Florideae will germinate in complete darkness, although growth soon comes to a standstill; it can, however, be resumed if the germlings are exposed to light before the sojourn in darkness has been too prolonged. Direct sunlight kills the spores very rapidly.

As regards the method of germination, the bipolar type, characteristic of Ceramiales, where the elongating spore divides into a rhizoid and the first cell of an erect-growing thread (fig. 185 D–F), is sharply opposed to that found in other Florideae, where division takes place primarily at right angles to the substratum and leads to the production of a prostrate thread or cushion (fig. 151 E–G). Kylin and others ((129) pp. 324, 507) here distinguish two or more types, viz.

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(*a*) that found in many Nemalionales and diverse Cryptonemiales in which a tubular prolongation from the spore segments to form a prostrate thread (fig. 151 C–G), while the original spore-body, often depleted of its contents, remains undivided, and (*b*) that found in Gigartinales, Rhodymeniales, Corallinaceae and most Cryptonemiales, in which the spore itself divides by diversely orientated walls to form a cushion-like mass (fig. 167 I–K). It may be doubted whether these differences are as fundamental as that between the method of germination of the Ceramiales and of other Florideae. Details of the process in individual forms have been given in the foregoing consideration of thallus-structure.

2. The Haplobiontic Types (Nemalionales)

(*a*) *Sexual Reproduction and Carpospore-formation*

The simplest reproduction among Florideae is met with in *Acrochaetium*.[1] Many species are monoecious, although *A. corymbiferum* and *A. rhipidandrum*, for instance, are dioecious, the male individuals of the former being smaller than the female. There is no special carpogonial branch and the lageniform carpogonia (fig. 227 A, *cp*) are seated laterally on the filaments or terminate branchlets, which may simultaneously bear protandrous antheridia (*A. Thuretii*, *A. efflorescens* ((368) p. 115) or even sporangia; in *A. gynandrum* ((558) p. 89) antheridia are inserted on the carpogonia, while in *A. efflorescens* the latter may occur in an intercalary position. In *A. violaceum* (fig. 227 C) the hypogynous cell bears a few branches (*br*) which elongate considerably after fertilisation. The oblong or spherical antheridia (fig. 227 F, *a*) are grouped at the apices of short laterals. In *Kylinia* ((558) p. 143), in which the carpogonia are incompletely known, the antheridia are borne on narrow little-pigmented cells arising vertically from the creeping threads.

After fertilisation the basal part of the carpogonium of *Acrochaetium* (fig. 227 B) lengthens and the trichogyne (*t*) is pushed to one side. The former (*cp*) undergoes one or more transverse divisions, and the resulting cells give rise to gonimoblast-threads (*g*); in *A. violaceum* (fig. 227 C), however, four or five threads (*g*) arise from the apex of the carpogonium without any septation of the latter. The gonimoblast-threads are generally branched (fig. 227 E), the terminal cells usually alone producing sporangia (*ca*); in *A. efflorescens*, for instance, carpospores are formed also from other cells of the threads.

The sexual reproduction of *Batrachospermum*[2] is very similar. The carpogonia (fig. 227 G) are terminal on branchlets arising from the

[1] See (68) p. 16, (177) p. 445, (254) p. 19, (387) p. 7, (389) p. 5, (558) p. 84, (632) p. 157 (*Balbiania*).

[2] See (17), (67) p. 144, (165), (326) p. 110, (370), (378) (506), (582), (586) p. 227, (630), (650). The account of gonimoblast-origin in the last of these is not altogether correct.

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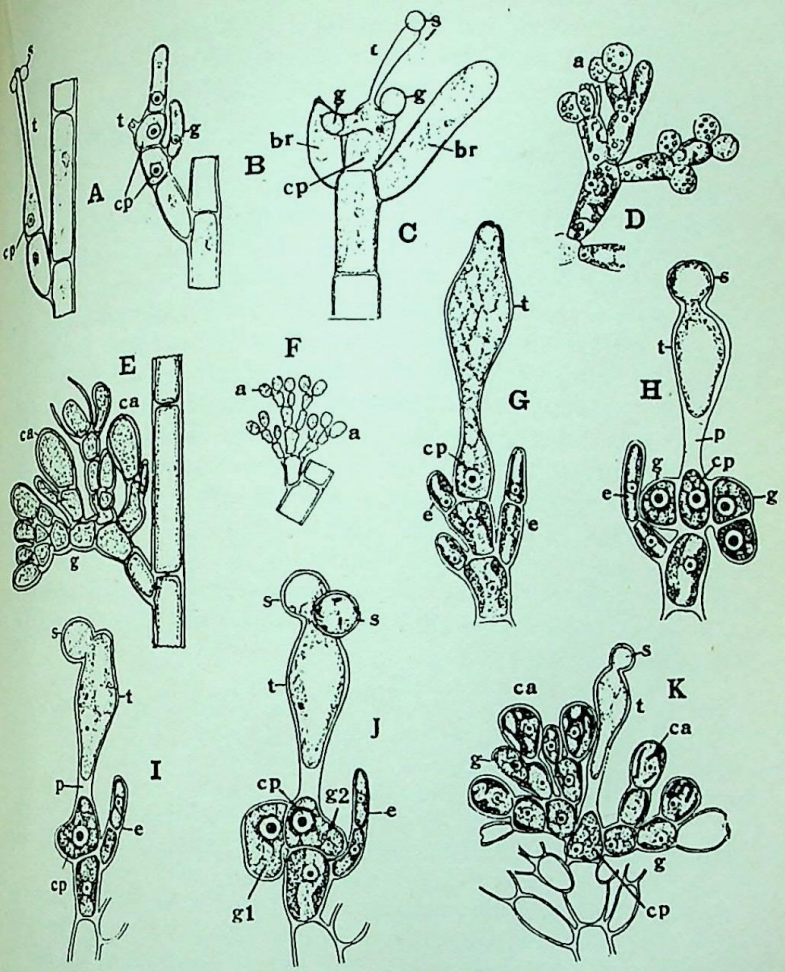

Fig. 227. A–C, E, F, *Acrochaetium*; A, B, E, F, *A. corymbiferum* (Smith) C. Ag.; C, *A. violaceum* (Kütz.). A, mature carpogonium; B, division of fertilised carpogonium (*cp*); C, early stage of gonimoblast-development; E, gonimoblast with ripe carposporangia; F, group of antheridia. D, G–K, *Batrachospermum moniliforme* Roth; D, group of antheridia; G, mature carpogonium; I, early stage of gonimoblast-development; J and H, later stages; K, mature gonimoblast with carposporangia. *a*, antheridia; *br*, branch; *ca*, carposporangium; *cp*, carpogonium; *e*, enveloping threads; *g*, gonimoblast; *p*, plug separating carpogonium and trichogyne; *s*, spermatium; *t*, trichogyne. (C after Drew; the rest after Kylin.)

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basal cells (*B. vagum*) or also from other internal cells of the primary whorled laterals; they are sometimes borne on cortical threads. The trichogyne (*t*) is separated from the body of the carpogonium (*cp*) by a constriction and, though commonly club-shaped, varies considerably in form, a feature which affords a valuable diagnostic character ((370) p. 5, (631) p. 131); a trichogyne nucleus has not been observed.[1] The spherical antheridia (fig. 227 D, *a*) are formed in small groups at the tips of the ultimate laterals.

One of the products of meiosis of the zygote-nucleus passes into a lateral outgrowth (fig. 227 I, *cp*) and becomes cut off as the first gonimoblast-initial (fig. 227 J, *g1*). The other daughter-nucleus divides again, and this results in the formation of a second initial (*g2*) on the opposite side of the carpogonium; further initials may be produced in the same way. They grow out into branched threads (fig. 227 K), the dilated terminal cells of which constitute carposporangia (*ca*). The gonimoblasts are commonly short and compact (cf. fig. 150 C, *ca*), but in a few species (*B. orthostichum* Skuja (641) p. 83) some of the branches extend over the internodes and there produce further groups of carposporangia; in *B. ectocarpum* the mature gonimoblasts sometimes project beyond the surface. The cells of the carpogonial branch usually bear laterals (fig. 227 G–J, *e*) which, in *B. moniliforme* and related species, form a loose envelope around the mature gonimoblasts; this is more marked in *Nothocladus* (p. 738). The trichogyne is very persistent (fig. 227 K).

The carpogonia (fig. 228 E, *cp*) of *Sirodotia* ((370) pp. 7, 38, (640) p. 298) possess a characteristic abaxial dilation (*d*) within which the female nucleus (*f*) is situated. A more important difference is that the few gonimoblast-threads (fig. 228 F, *g*) extend over the internodes (fig. 228 G), bearing short branch-systems, the terminal cells of which (*ca*) form carpospores (cf. *Batrachospermum orthostichum*); in *S. suecica* the single gonimoblast-thread arises adaxially.

Similar elongate gonimoblasts, extending horizontally through the cortex, occur in *Cumagloea* ((233) p. 398, (387) p. 10) and *Dermonema* ((599) p. 334, (681) p. 34); in the last (fig. 228 D, *g*) they show considerable ramification and bear vertical branch-systems, the end-cells of which form club-shaped carposporangia (*ca*). The carpogonial branches (*cb*) are here three-celled. The possession of elongate gonimoblasts does not probably imply any close relationship between the various genera, which differ considerably in vegetative structure (see also *Nothocladus*, p. 738). It is still an open question whether the penetration of the threads among the vegetative branches of the thallus is associated with any absorption of nutriment from the latter.

Among the multiaxial Nemalionales, *Helminthocladia* closely resembles *Batrachospermum* in its reproduction ((201) p. 90, (389) p. 6,

[1] The nucleus recorded by Davis ((165) p. 53) is possibly the second spermatial nucleus (cf. his fig. 27).

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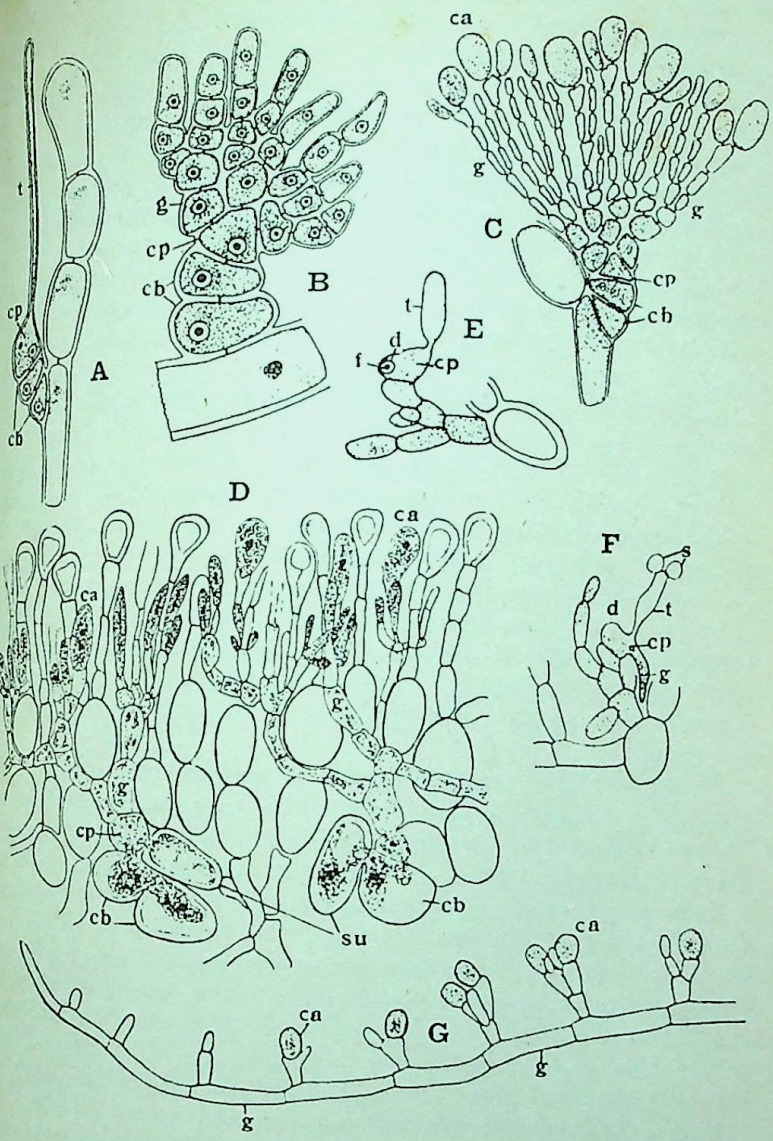

Fig. 228. A–C, *Helminthocladia Calvadosii* (Lamour.) Setch.; A, mature carpogonium; B, young and C, mature gonimoblast. D, *Dermonema gracile* (Mart.) Schmitz, parts of two gonimoblasts. E–G, *Sirodotia suecica* Kylin; E, carpogonial branch and carpogonium; F, early development of gonimoblast; G, part of mature gonimoblast. *ca*, carposporangium; *cb*, carpogonial branch; *cp*, carpogonium; *d*, process on carpogonium; *f*, female nucleus; *g*, gonimoblast; *s*, spermatium; *su*, supporting cell; *t*, trichogyne. (D after Svedelius; the rest after Kylin.)

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(558) p. 148), although the usually three-celled carpogonial branches (fig. 228 A, *cb*) are better defined. In *H. Calvadosii* the fertilised carpogonium cuts off by approximately longitudinal walls (fig. 228 B) a number of cells which give rise to compact gonimoblasts (fig. 228 C) with terminal carposporangia (*ca*), while in *H. Papenfussii* ((401) p. 4, (450) p. 239) the first division is almost transverse; this species is also distinguished by the fusion of the cells of the carpogonial branch after fertilisation. There may or may not be an envelope of sterile filaments.

Acrochaetium, *Batrachospermum*, and *Helminthocladia* exhibit primitive characteristics in the usual absence of any post-sexual fusions, in the customary formation of carpospores only from the terminal cells of the gonimoblasts, and in the lack of a clearly defined envelope around the latter. Scarcely more specialisation is evident in *Lemanea* ((22) p. 203, (380) p. 8, (629) p. 21), where (fig. 229 C) the carpogonial branches (*cb*) differentiate simultaneously with the cortex (*c*), arising from the cells of the longitudinal threads referred to on p. 464 (cf. also fig. 156 L, *cb*). In *Tuomeya* the carpogonial branches are spirally twisted and arise from the basal cells of the laterals. According to Atkinson those of *Lemanea* are usually situated near the primary laterals (basal cells) in *Eulemanea*, whereas in *Sacheria* they commonly lie remote from them, sometimes even occurring within the antheridial zones. The carpogonial branch (fig. 229 A, B, D, *cb*) consists of a variable number of cells (in *Eulemanea* often bearing short branches), embedded within the wall, while the trichogyne (*t*), which is occasionally forked, projects slightly beyond the surface of the bristle.

The oblong antheridia (fig. 229 F, *a*) are generally formed in pairs upon cylindrical mother-cells (*am*), which are crowded together at the "nodes" (fig. 229 G–J, *a*) and terminate branches of the longitudinal threads. In *Eulemanea*, where the latter are profusely branched, the antheridial sori form rings (fig. 229 I, J, *a*), but in *Sacheria* they occupy the summits of projections (fig. 229 G, H, *a*) which are arranged in a verticillate manner. The young mother-cell usually bears a unicellular hair (fig. 229 F, *h*) which is pushed aside by the developing antheridia. Fertilisation apparently occurs during the early months of the year.

The fertilised carpogonium enlarges and cuts off, on its inner side, a succession of initials which project into the central cavity and give rise to branched gonimoblast-threads, most of the cells of which form carposporangia (fig. 229 E, *ca*). The nearly colourless carpospores are liberated by decay of the thallus.

Greater specialisation is shown by *Nemalion*, of which *N. helminthoides* and *N. multifidum* have been repeatedly investigated.[1] The plants are commonly dioecious, the male being smaller than the female. The carpogonial branches (fig. 230 A) are constituted by

[1] See (67) p. 141, (136), (326) p. 113, (365) p. 323, (377), (746), (748). Certain details relating to other species are given by Boergesen ((50) p. 61).

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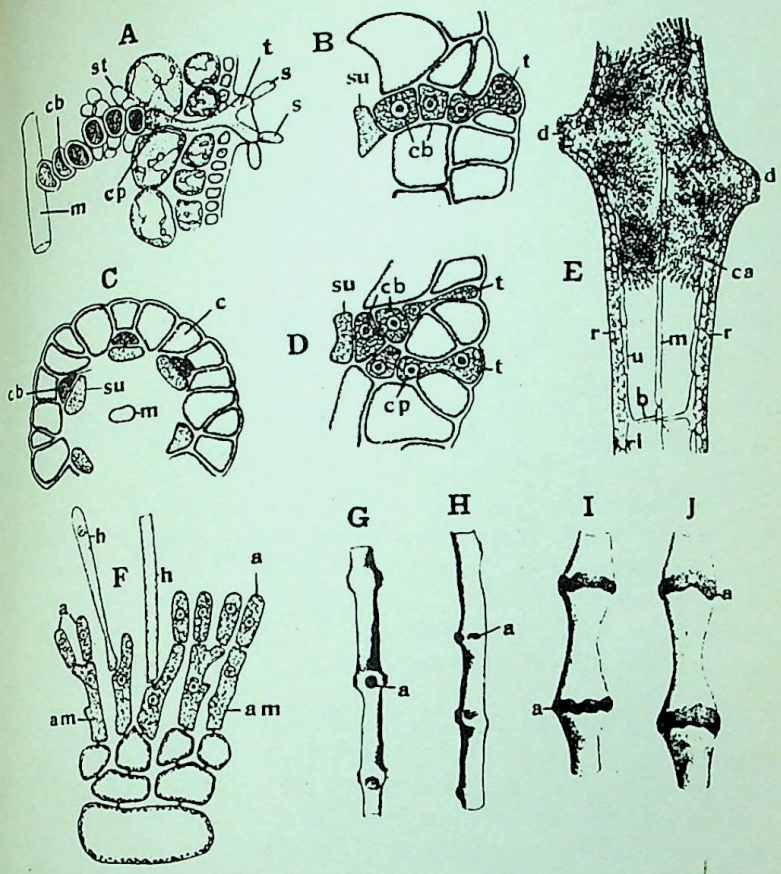

Fig. 229. *Lemanea*; A, *L. australis* Atk.; B–D, F, H, *L. fluviatilis* C. Ag.; E, G, *L. mamillosa* Kütz.; I, *L. annulata* Kütz; J, *L. nodosa* Kütz. A, longitudinal section of small part of bristle, carpogonial branch and carpogonium; B, young carpogonial branch; C, transverse section of a young segment, showing early stage in development of carpogonial branches; D, carpogonial branch bearing two carpogonia; E, longitudinal section of a bristle, with ripe gonimoblasts; F, development of antheridia; G–J, parts of bristles showing arrangement of antheridial sori. *a*, antheridia or antheridial sori; *am*, antheridial mother-cell; *b*, basal cell of lateral; *c*, cortex; *ca*, carposporangia; *cb*, carpogonial branch; *cp*, carpogonium; *d*, "node" (meeting point of ascending and descending longitudinal threads); *h*, hair; *l*, descending and *u*, ascending longitudinal threads; *m*, axial cell; *r*, surface-layer of thallus; *s*, spermatium; *st*, sterile threads on carpogonial branch; *su*, supporting cell; *t*, trichogyne. (A, E after Atkinson; G–J after Sirodot; the rest after Kylin.)

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ordinary laterals and consist of 4–7 cells, the upper of which (*hy*) are nutritive cells with only a minute colourless plastid, while the lower bear a number of ordinary branches (*l*). The elongate trichogyne (*t*) projects slightly beyond the surface of the thallus. The antheridia are formed on branches, which arise from the terminal cells of the laterals (fig. 230 A, *a*) and consist of 2–4 cells (fig. 230 F, *ab*) with non-pigmented plastids and abundant contents; each cell produces 3 or 4 antheridia (*a*) around its apex. One or both male nuclei (cf. p. 597) pass into the trichogyne.

Soon after sexual fusion the large zygote-nucleus undergoes meiosis and the chromatophore divides. Thereupon the carpogonium segments transversely into two cells (fig. 230 B), the upper of which (*cp 1*) produces the gonimoblasts. Its nucleus divides again and one half passes into a lateral protuberance, which is cut off as a gonimoblast-initial; this is repeated several times so that a number of initials (fig. 230 C, *i*) are produced. The lower carpogonial cell (*cp 2*) gradually fuses with the hypogynous cells (fig. 230 C, D, *hy*) and these with the underlying cells (fig. 230 E, *f*), a process accompanied by nuclear degeneration and one by means of which the nutriment in these cells is no doubt rendered available to the developing gonimoblasts. The threads, formed from the gonimoblast-initials (fig. 230 E, *g*), hang down parallel with the carpogonial branch and each of their cells produces on its outer side an upwardly curved 2–3-celled branchlet, the terminal cell of which enlarges to form a sporangium (*ca*); frequent proliferation of the sporangia is recorded ((136) p. 339, (748) p. 620).

The higher differentiation of *Nemalion* is shown by the presence of nutritive cells in the carpogonial branch, by the development of gonimoblasts from the upper half of the carpogonium only, by the marked fusions that occur subsequent to fertilisation, and by the special form of the gonimoblasts. Only one of the two nuclei formed in the first meiotic division is supposed to divide again (cf. however (136) p. 339, (748) p. 619). The reproduction of most species of *Liagora* ((50) p. 69, (51) p. 43, (389) p. 9) is in all essentials like that of *Nemalion*.

Other Helminthocladiaceae, of which *Helminthocladia*, *Cumagloea* and *Dermonema* (p. 610) have already been considered, are less specialised than *Nemalion*, although Svedelius ((681) p. 32) records occasional fusion of the fertilised carpogonium with the supporting cell of the carpogonial branch in *Dermonema* (cf. fig. 228 D, on the left). In *Trichogloea* (91) the enlarged hypogynous cell functions as a nutritive cell. The dioecious *Helminthora divaricata*[1] shows much the same features as *Nemalion* (cf. fig. 230 G), although fusion with the hypogynous cells is not so marked and the gonimoblasts become enveloped by sterile branches (fig. 159 C, *cy*; 230 I, *e*) which arise from the second and third cells of the four-celled carpogonial branch (fig. 230 H). Such

[1] See (67) p. 142, (326) p. 114, (365) p. 317, (387) p. 8, (673) p. 221, (692) p. 64.

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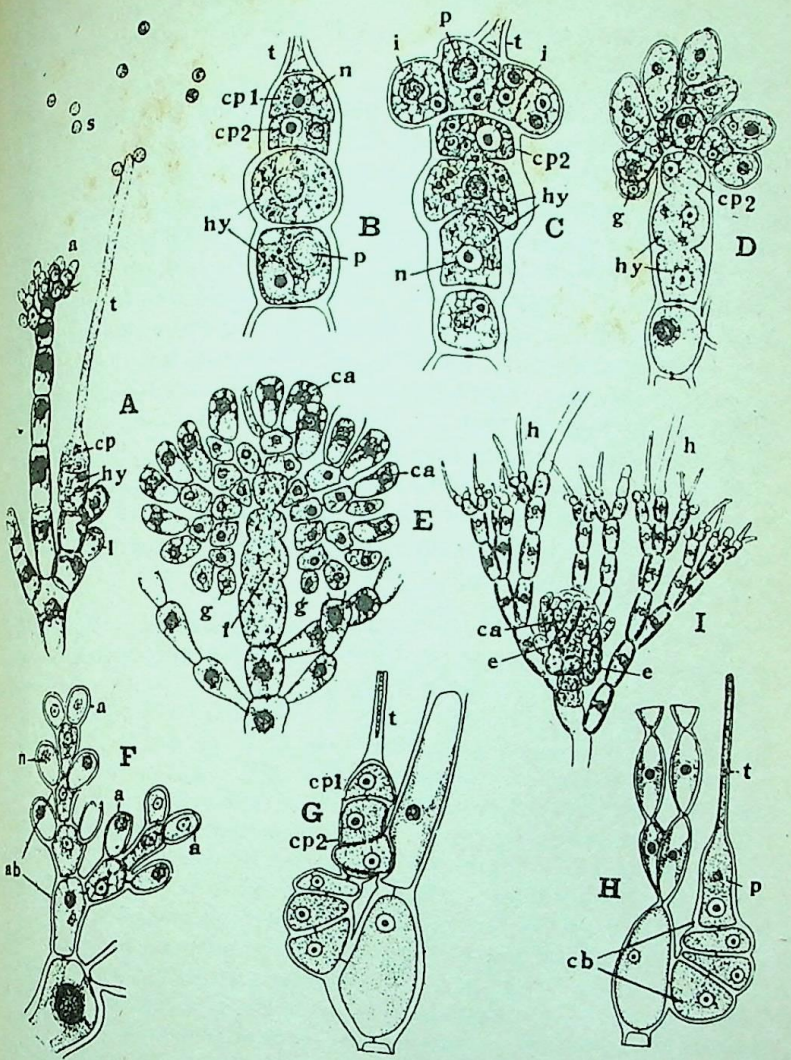

Fig. 230. A–F, *Nemalion multifidum* (Web. & Mohr) J. Ag.; A, part of a branch-system, with antheridia and mature carpogonium; B, first division of fertilised carpogonium (*cp1*, *cp2*); C, formation of gonimoblast-initials; D, later stage of development of gonimoblasts; E, mature gonimoblast; F, antheridial branch (*ab*). G–I, *Helminthora divaricata* J. Ag.; G, first division of fertilised carpogonium (*cp1*, *cp2*); H, mature carpogonium; I, branch-system, with ripe gonimoblasts. *a*, antheridia; *ca*, carposporangia; *cp*, carpogonium; *e*, enveloping threads; *f*, fusion-cell; *g*, gonimoblast; *h*, hair; *hy*, hypogynous cells; *i*, gonimoblast-initial; *l*, lateral; *n*, nucleus; *p*, pyrenoid; *s*, spermatium; *t*, trichogyne. (A and I after Thuret & Bornet; the rest after Kylin.)

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an envelope is also found in *Trichogloea* and indicated in *Nemalion* ((387) p. 8). The antheridia of *Helminthora* form groups on the terminal cells of the laterals (cf. also (85) p. 258). All Helminthocladiaceae appear to have terminal carpospores.

The Naccariaceae and Bonnemaisoniaceae, which show the greatest vegetative specialisation among Nemalionales (p. 479), also afford evidence of advance in reproduction, although there is no complete parallel. Here the hypogynous cell of the carpogonial branch bears short laterals composed of nutritive cells with dense contents (figs. 231 A, B; 232 B, D, *nu*), which are gradually exhausted during the development of the gonimoblast. Except in *Atractophora*, the fertilised carpogonium (fig. 231 F, *cp*) fuses with the hypogynous cell (*hy*) and establishes a direct connection with this nutritive system, but in *Bonnemaisonia* and *Asparagopsis* the fusions after fertilisation are more comprehensive than in Naccariaceae. In these two genera, moreover, threads originating from cells of the carpogonial branch, and more particularly from adjacent cells, combine to form a compact investment around the gonimoblast (fig. 232 B, *e*). For such a fructification, provided with a special protective envelope, the term *cystocarp* is often reserved.

In Naccariaceae the fertile branches at first develop few laterals and exhibit little hypha-formation. The three-celled carpogonial branches (fig. 231 A, *cb*) of *Atractophora* ((68) p. 50, (387) p. 13, (766) p. 401) and the two-celled ones (fig. 231 D, *cb*) of *Naccaria* ((68) p. 52, (387) p. 14, (586) p. 229, (766) p. 394) arise from basal cells (*su*) of laterals which also bear short branches; the small nutritive cells (fig. 231 B, E, *nu*) are cut off from the hypogynous cells. In *Atractophora* (fig. 231 B) the fertilised carpogonium (*cp*) fuses with the supporting cell (*su*), while in *Naccaria* (fig. 231 F, G) the pit-connection between the former (*cp*) and the hypogynous cell (*hy*), and sometimes those between the latter and some of the nutritive cells, gradually widen (cf. *Bonnemaisonia*).

The gonimoblast-threads arise from the carpogonium itself, singly in *Naccaria* (fig. 231 F, *g*), to the number of two or three in *Atractophora* (fig. 231 C, *g*). Branching extensively, they spread upwards and downwards and form an investment around the axial threads of the fertile tract (fig. 231 C; cf. *Sirodotia*, *Cumagloea*); their perpendicular branches bear terminal sporangia. The photosynthetic laterals, amid which these branches spread, exhibit abundant ramification, but this is much more marked in *Naccaria*, where the fertile tracts appear as ellipsoidal swellings on the fronds. Numerous hyphae arise so that the internal tissue of these swellings constitutes a dense pseudo-parenchyma, which is surrounded by a broad and more loosely organised cortical region covered by an envelope of mucilage. The gonimoblast-threads of *Naccaria* are stated to form secondary pit-connections with the central cells and other elements of the fertile tract ((766) p. 396).

The antheridial mother-cells are terminal on branches arising mainly from the basal cells of the laterals; in *Atractophora* the entire lateral may

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be involved. In *Naccaria*, owing to slight elongation of the axial cells, the antheridial sori often constitute extensive colourless areas interrupted only by the projecting pigmented tips of the sterile branches.

The Bonnemaisoniaceae, though more specialised, show considerable resemblances to *Naccaria*. *Bonnemaisonia asparagoides* ((87) p. 297, (376) p. 551, (679) p. 39)[1] is monoecious,[2] while the species of *Asparagopsis* ((50) p. 355, (141) p. 143, (387) p. 24, (679) p. 18) are dioecious. The sex organs are borne on secondary laterals of limited growth (p. 480) which alternate irregularly; in *Bonnemaisonia* (fig. 232 G, *m*) they arise directly from them, while in *Asparagopsis* they are

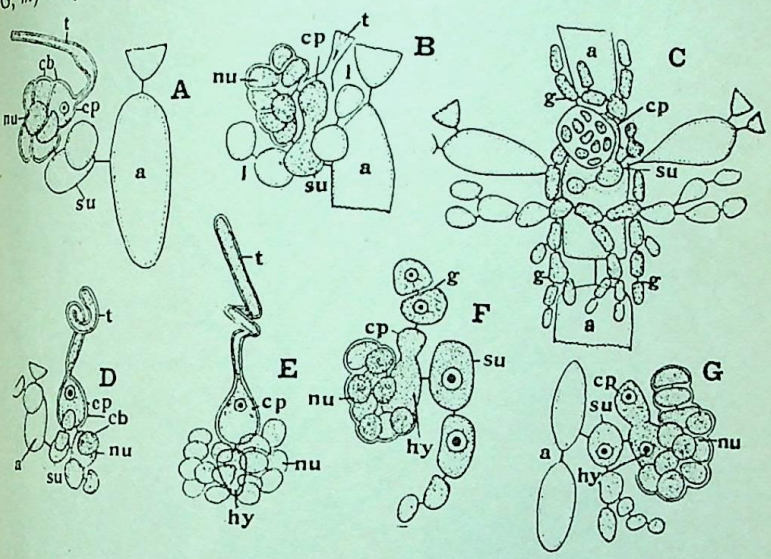

Fig. 231. A–C. *Atractophora hypnoides* Crouan; A, mature carpogonium; B, fusion between carpogonium (*cp*) and supporting cell (*su*); C, young gonimoblasts. D–G, *Naccaria Wigghii* (Turn.) Endl.; D, young and E, mature carpogonium; F, young gonimoblast; G, fusion between carpogonium (*cp*) and hypogynous cell (*hy*), immediately after fertilisation. *a*, axial cells; *cb*, carpogonial branch; *cp*, carpogonium; *g*, gonimoblast; *hy*, hypogynous cell; *l*, lateral; *nu*, nutritive cells; *su*, supporting cell; *t*, trichogyne. (After Kylin.)

situated upon their branches. In the male shoots of *A. armata* nearly all the secondary branches produce antheridia. The male branch consists of a limited number of elongate axial cells, nearly all of which (*Asparagopsis*) or only the upper (*Bonnemaisonia*) cut off pairs of pericentrals which alternate in successive segments;[3] the laterals to which they give rise combine to form a continuous layer of mother-cells, each producing two or three antheridia (fig. 222 H). In the

[1] Phillips ((518) p. 349) gives a few details about the female branches.
[2] The dioecious form ((65) p. 298, (114)) is suspected of being a distinct species ((265) p. 104).
[3] Kylin describes the structure differently in *Bonnemaisonia*.

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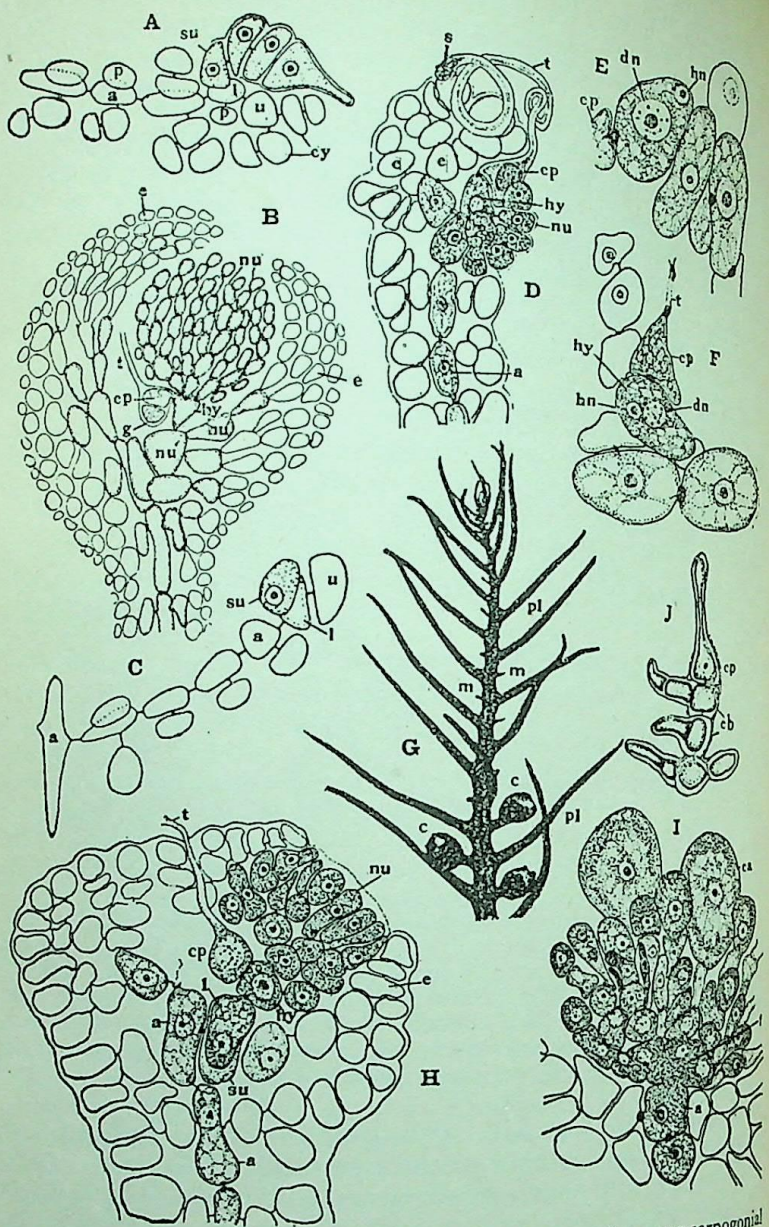

Fig. 232. A, C, *Asparagopsis hamifera* (Hariot) Okam.; A, young carpogonial branch; C, formation of supporting cell. B, D, G–I, *Bonnemaisonia asparagoides* (Woodw.) Ag.; B, young cystocarp, formation of gonimoblast-initial; D, mature carpogonial branch and carpogonium; G, lateral with basal cystocarps (*c*) and antheridial branches (*m*); H, older carpogonium, development of nutritive threads; I, older gonimoblast showing fusion of lower cells. E, F, *Asparagopsis armata* Harv.; E, diploid nucleus in diakinesis within the hypogynous cell; F, diploid nucleus in hypogynous cell, carpogonium still persisting. J, *Chaetangium saccatum* (Lamour.) J. Ag., carpogonial branch.

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female shoots of *Bonnemaisonia* all except the terminal cell become corticated and later form the stalk of the solitary cystocarp (fig. 232 G, *c*). Those of *Asparagopsis* produce only two fertile laterals, representing the secondary laterals of two successive basal segments, so that the resulting cystocarps are usually at right angles to one another.

In both genera the terminal cell of the female axis divides obliquely (fig. 232 C), the upper segment (*u*) producing three groups of laterals (fig. 232 A, *cy*) which participate in the formation of the cystocarp-wall, while the lower (*l*) cuts off three pericentrals, one of which acts as the supporting cell (*su*) of the three-celled carpogonial branch (fig. 232 C, *su*); in *Bonnemaisonia* the trichogyne (fig. 232 D, *t*) is long and spirally twisted. The cystocarp-wall (fig, 232 B, H, *e*), which develops to a considerable degree already prior to fertilisation, is completed by laterals arising from all three pericentrals, as well as from the first cell of the carpogonial branch. The hypogynous cell (fig. 232 D, H, *hy*) gives rise to laterals, composed of nutritive cells (*nu*) which enlarge and increase in number subsequent to sexual fusion. During the early divisions in the fertilised carpogonium the nutritive cells fuse both with one another and with the hypogynous cell, thus furnishing material for the development of the gonimoblast (cf. *Naccaria*).

In *Bonnemaisonia* the reduction divisions take place in the carpogonium, but only one of the four resulting nuclei probably persists. The gonimoblast-initial (fig. 232 B, *g*) is cut off internally from the carpogonium (*cp*), adjacent to a group of large cells full of nutriment (*nu'*) occupying the floor of the young cystocarp. The initial divides rapidly to form a several-layered disc and, as this happens, the nutritive threads (*nu*) connected with the hypogynous cell lose their contents. Later the lower cells of the gonimoblast-disc fuse with one another, with the nutritive cells (*nu'*) below, and with the supporting cell of the carpogonial branch (sometimes also with the fertile axial cell) to form a large multinucleate fusion-cell occupying the floor of the cystocarp (fig. 232 I, *f*). The overlying gonimoblast-cells give rise to branched threads, the end-cells of which form sporangia (*ca*). The stalked cystocarps (fig. 232 G, *c*), which have a terminal aperture, stand opposite the primary laterals (*pl*); according to Golenkin (1251) p. 258) they bear plentiful vesicular cells.

The fusion-nucleus of *Asparagopsis* passes into the hypogynous

---

a, axial cell; *c*, cystocarp; *ca*, carposporangium; *cb*, carpogonial branch; *cp*, carpogonium; *cy* and *e*, cystocarp-envelope; *dn*, diploid and *hn*, haploid nucleus; *f*, fusion-cell; *g*, gonimoblast-initial; *hy*, hypogynous cell; *l*, lower segment of terminal cell; *m*, male branches; *nu*, *nu'*, nutritive cells; *p*, pericentral; *pl*, primary lateral; *s*, spermatium; *su*, supporting cell; *t*, trichogyne; *u*, upper segment of terminal cell. (A–C after Kylin; J after Martin; the rest after Svedelius.)

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cell, while the carpogonium itself degenerates (fig. 232 E, F). Within the hypogynous cell the diploid nucleus (*dn*) enlarges and undergoes meiosis (fig. 232 E). During the development of the two (or more?) gonimoblasts a large fusion-cell similar to that of *Bonnemaisonia* is formed at the base of the cystocarp, bearing on its upper side the carposporangial threads which are here interspersed with sterile filaments. The axial cells in the lower part of the fertile branch have abundant contents and wide pit-connections.

A similar specialisation is found among the multiaxial Nemalionales in the Chaetangiaceae, of which the monoecious *Scinaia furcellata* has been fully investigated ((671); cf. also (68) p. 19, (617)). The antheridial branches (fig. 233 F, *br*) arise from the pigmented end-cells (*p*) of the laterals (p. 471), the mother-cells (*m*), which produce two or three antheridia (*a*), being embedded in a layer of mucilage (*mu*) formed by the outer walls of the vesicular cells (*c*). The three-celled carpogonial branches (fig. 233 A) originate from the loose internal tissue just behind the apex. At an early stage the hypogynous cell (fig. 233 B, D, *hy*) divides longitudinally into four large cells (fig. 233 I) which possess dense contents and often contain several nuclei, while the first cell of the branch produces a few short threads (*e*).

After fertilisation (fig. 233 C, D) the fusion-nucleus (*dn*) passes from the carpogonium (*cp*) through the enlarged pit-connection (*po*) into one of the four hypogynous cells and there undergoes meiosis (fig. 233 E, J). Three of the resulting nuclei gradually degenerate (fig. 233 H, I, *te*), while the fourth passes into the single gonimoblast which arises from the upper end of the hypogynous cell (fig. 233 H, *g*). The gonimoblast penetrates through the pit-connection into the empty carpogonium and, piercing the latter on one side, soon commences to branch. In the meantime the threads arising from the first cell of the carpogonial branch (fig. 233 E, J, *e*) multiply and form a compact envelope (fig. 233 K, *e*). The hypogynous cells (*hy*) partially fuse and flatten out against the latter, while the gonimoblast gradually fills most of the space within it. Many of its branches produce rows of 2–4 sporangia (fig. 233 G, *ca*), while others (*st*) remain sterile (cf. *Asparagopsis*). The dark-coloured spherical cystocarps, which are provided with an apical aperture, are sunk within the surface of the thallus.

The mature cystocarps of *Galaxaura* (711) and *Chaetangium* ((599) p. 338) are similarly embedded. The lower cells of the carpogonial branch of *C. saccatum* ((449) p. 119) bear short laterals (fig. 232 J; cf. Bonnemaisoniaceae). Later the carpogonium degenerates, although the underlying cell survives, while the cells of its laterals increase considerably in size. On somewhat slender data Martin concludes that, as in *Scinaia*, the diploid nucleus passes into the hypogynous cell, with subsequent formation of a tetrad by reduction, although there is no good evidence of the occurrence of fertilisation. The richly branched

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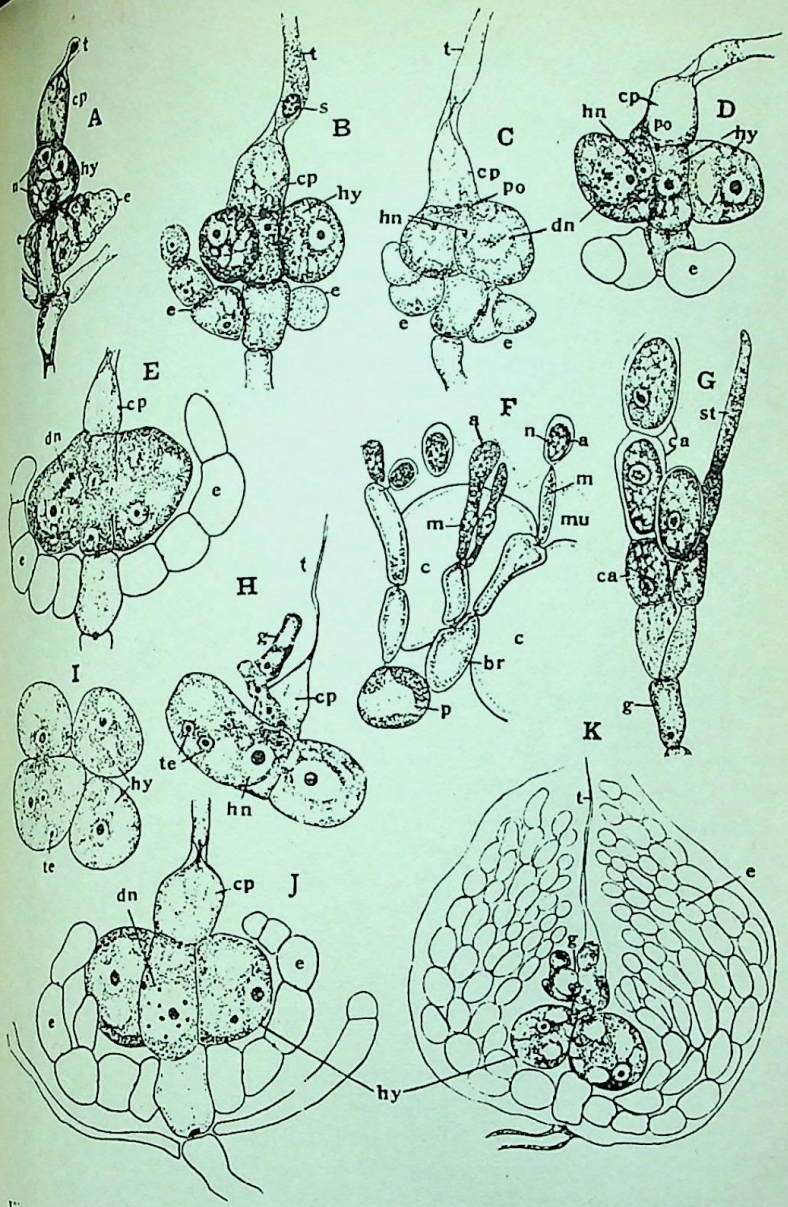

Fig. 233. *Scinaia furcellata* (Turn.) Bivona (after Svedelius). A, young carpogonium; B, fertilisation; C, D, diploid nucleus (*dn*) has passed through connection (*po*), between carpogonium and hypogynous cell, into the latter; E, division of diploid nucleus; F, formation of antheridia; G, part of a mature gonimoblast; H, early development of gonimoblast; I, transverse section through the hypogynous cells, the one containing nuclei of the tetrad (*te*); J, diploid nucleus (*dn*) in diakinesis within hypogynous cell; K, vertical section of very young fruit. *a*, antheridia; *br*, branch; *c*, vesicular cell; *ca*, carposporangia; *cp*, carpogonium; *dn*, diploid nucleus; *e*, enveloping threads; *g*, gonimoblast; *hn*, haploid nucleus; *hy*, hypogynous cells; *m*, antheridial mother-cell; *mu*, mucilage; *n*, nucleus; *p*, photosynthetic cell; *po*, pore connecting carpogonium and hypogynous cell; *s*, spermatium nucleus; *st*, sterile thread of gonimoblast; *t*, trichogyne; *te*, nuclei of tetrad.

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gonimoblast arises from the hypogynous cell, some of its branches interweaving to form a "wall", while others produce the carpospores; there is no true envelope, the laterals on the lower cells of the carpogonial branch disappearing during the development of the gonimoblast. A narrow pore is formed above the resulting fruit.

The antheridia of *Galaxaura* ((50) p. 112, (51) p. 75, (342) p. 21) are formed in large numbers from the ends of richly branched filaments, which arise from the floor and sides of deep and often wide cavities (cf. Corallinaceae). The antheridial filaments originate close to the apex ((682) p. 595) and are gradually overgrown by adjacent sterile threads; the aperture, which progressively widens, results from degeneration of the overlying cells. Similar antheridial cavities, in part very small, occur in *Chaetangium* ((448) p. 171).

(*b*) *General Survey of the Life-cycle*

Kylin emphasises that the uniaxial and multiaxial Nemalionales must be regarded as distinct developmental series, a point of view which receives considerable support from a consideration of their reproductive features. In each series definite nutritive cells are differentiated only in the more specialised forms, viz. the uniaxial Naccariaceae and Bonnemaisoniaceae, and the multiaxial Chaetangiaceae; it is, moreover, only in the two last families that a compact envelope is formed around the gonimoblast leading to the formation of a true cystocarp. In *Acrochaetium*, *Batrachospermum*, and *Lemanea* there is no fusion of the carpogonium with other adjacent cells after fertilisation, such as obtains in some of the less specialised multiaxial forms—the Helminthocladiaceae. Here, however, only the carpogonial branch itself (fig. 230 D, E) serves to provide nutriment for the developing gonimoblast, although the outgrowth of gonimoblast-threads among the photosynthetic laterals in *Dermonema* (fig. 228 D) and *Cumagloea* (cf. also Naccariaceae) perhaps represents another means of attaining the same end. In Naccariaceae and Bonnemaisoniaceae, on the other hand, special nutritive cells (figs. 231 A, D; 232 B, H, *nu*) are formed from the hypogynous cell and this is also so in *Scinaia*. Except in *Atractophora*, these cells fuse with one another during the post-fertilisation development.

The gonimoblasts in Nemalionales usually originate from the carpogonium itself, but in *Asparagopsis*, *Scinaia*, and perhaps in *Chaetangium*, the diploid nucleus passes into a hypogynous cell and it is from this that the gonimoblast arises. The post-fertilisation behaviour of the diploid nucleus in these genera is analogous to that found in many diplobiontic Florideae, and there seems no valid reason why the hypogynous cell that receives it should not be termed an auxiliary cell ((449) p. 139, (679) p. 49, (741*a*); cf. however (389) p. 92, (398) p. 140). It appears that the haplobiontic Florideae, despite the fundamental difference in their life-cycle, show in the sexual reproduction of the

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more advanced forms many of the specialised features that characterise the diplobiontic type, and it may be recalled that the vegetative construction of the genera involved also affords indications of advance (cf. p. 479).

In *Nemalion* (fig. 230 E) and *Asparagopsis* several gonimoblast-threads are produced, so that at least two of the four nuclei formed at the reduction division are utilised, while in *Scinaia* (fig. 233 H, I), and probably also in *Bonnemaisonia* ((679) p. 46) and *Chaetangium* ((449) p. 138), all but the one employed in the formation of the single gonimoblast degenerate. The last-named genera are in this respect more specialised than other Nemalionales. In *Batrachospermum* all four nuclei are apparently used.

Since Svedelius ((671) p. 32) showed that reduction occurs at the first divisions of the zygote-nucleus in *Scinaia*, this has been demonstrated for several other Nemalionales. Reference may be made to the researches of Kylin ((377) p. 267) and Cleland ((136) p. 338) on *Nemalion multifidum*, whereby earlier erroneous statements of Wolfe were rectified, and the recent investigation of *Bonnemaisonia* and *Asparagopsis* by Svedelius ((679) pp. 27, 44). Evidence for the occurrence of reduction immediately after fertilisation has also been produced for *Batrachospermum* ((378) p. 161) and *Helminthora* ((387) p. 9), and it can hardly be doubted that this is the rule in Nemalionales. The zygote therefore represents the only diploid stage. What is known of other methods of reproduction in the majority of Nemalionales is in accord with these findings.

Such reproduction is most commonly effected by *monospores* which, despite the fact that some individuals may bear these structures only, are nearly always to be found also on plants bearing sex organs and producing carpospores ((347) p. 218). The monospores are in fact accessory reproductive cells (1, p. 51), which serve to reproduce the haploid phase, and are not an essential part of the life-cycle like the carpospores.

The monosporangia are spherical or oblong structures (fig. 234, *m*) which differ from the antheridia in their deeply pigmented contents and larger size. Those of *Acrochaetium* (fig. 234 A, *m*) are sessile or shortly stalked or sometimes grouped together at the ends of short lateral branch-systems (fig. 234 B, *m*). In many species of *Batrachospermum* they are confined to the juvenile stage (p. 456 and fig. 151 B, *m*), but in *B. sporulans* Sirod. and *B. vagum* ((262) p. 284, (370) p. 8, (631) p. 138, (633) p. 96), which rarely produce sex organs, as well as in the tropical *B. lochmodes* ((646) p. 620), for example, they occur, like the antheridia, at the apices of the laterals of the adult shoots (fig. 234 C, D, *m*). In *Helminthora* ((673) p. 215) they occupy the same position (fig. 234 E, *m*). The monosporangia of *Scinaia* ((671) p. 14) are formed (fig. 234 F, G, *m*) from the narrow pigmented cells that lie between the vesicular cells (*e*) in the younger parts. In Naccariaceae, Bonne-

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maisoniaceae, *Lemanea* and *Nemalion* no such structures are known. The "*Chantransia*-stages" of *Lemanea* are purely vegetative ((72) p. 193, (363) p. 200).

The monospores are liberated by rupture of the apex of the sporangium-wall (fig. 234 E); proliferation is probably not uncommon. Amoeboid movements of the naked monospores have been frequently reported ((154), (558) pp. 85, 101, (673) p. 218). They appear to germinate in the same way as the carpospores.

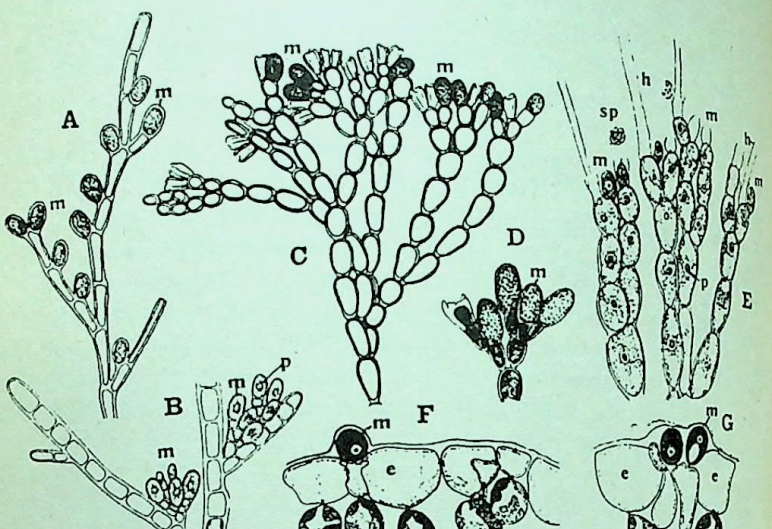

Fig. 234. Monospore-formation in Nemalionales. A, *Acrochaetium rhipidandrum* (Rosenv.). B, *A. Daviesii* (Dillw.) Naeg. C, D, *Batrachospermum lochmodes* Skuja. E, *Helminthora divaricata* J. Ag. F, G, *Scinaia furcellata* (Turn.) Bivona. *c*, chromatophores; *e*, vesicular cells; *h*, hairs; *m*, monospores; *p*, pyrenoids; *sp*, monospore. (A after Kylin; B after Taylor; C, D after Skuja; E–G after Svedelius.)

Diverse authorities ((633) p. 98, (671) pp. 18, 22) have commented on the similar positions of antheridia and monosporangia, which may even occur side by side on the same lateral. Transitions between the two kinds of organs are reported in *Batrachospermum* and *Scinaia*, while in *Helminthocladia* certain structures have been variously interpreted as arrested antheridial branches ((558) p. 147) and as monosporangia ((671) p. 18). The implications of these features are at present not clear.

In several species of *Liagora* small orbicular discs, with a gelatinous envelope and more or less calcified, occur immersed among the laterals. They bear monosporangia, sometimes showing division of the contents into two ((50) p. 456, (319)). It remains doubtful whether they are a stage in the development of *Liagora* or belong to an independent endophyte.

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Several species of *Acrochaetium* (*A. Daviesii*, *A. Thuretii*, *A. virgatulum*) bear tetrasporangia (fig. 235 B, E, *t*) as well as monosporangia, both usually occurring on the sexual plants ((45) p. 351, (369) p. 118, (558) p. 85). On the other hand, in *A. violaceum*[1] (fig. 235 E; (177)), and probably in *A. efflorescens*[2] (fig. 235 B; (368), (410), (558) p. 85), there are distinct tetrasporic and sexual individuals which may also bear monospores (fig. 235 A, *m*), although in *A. efflorescens* these often occur on distinct plants. There is, moreover, a certain seasonal alternation, since the tetrasporic individuals occur mainly during the colder and the sexual ones during the warmer months ((177) p. 448, (558) p. 137). The supposed asexual plants of *A. efflorescens* are smaller and less abundantly branched ((368) p. 118). The tetrasporangia of *Acrochaetium* are always cruciately divided and this is also so in *Rhodochorton* (fig. 235 D, H). In this genus tetrasporangia are the rule, although one instance of monosporangia has been recorded ((462) p. 374); no carpogonia are known, but Rosenvinge ((558) p. 389) has described antheridia in *R. penicilliforme*.

While *A. efflorescens* and *A. violaceum* may actually be diplobiontic, such a view cannot be accepted without a cytological investigation. In face of the known facts, moreover, it appears rather improbable. Although data as to the time at which reduction occurs are not available for *Acrochaetium*, it is generally assumed that it takes place during the first divisions of the zygote-nucleus. In species bearing tetrasporangia and monosporangia on the sexual plants reduction during tetraspore-formation is very unlikely. The occasional association of monosporangia with tetrasporangia on the non-sexual plants of *A. efflorescens* and *A. violaceum* renders it equally improbable that the tetrasporangia are here the seat of a reduction division. With our present knowledge it would seem most plausible to regard these tetrasporangia merely as divided monosporangia ((771); cf. also (347) p. 219), and in this connection attention may be drawn to the occurrence in certain species of bispores ((47) p. 179, (50) p. 43, (51) p. 20) and polyspores ((59) p. 38, (316) p. 88); in *A. multisporum* Boerges. the latter arise by further division of the four cells first formed.

Cruciate tetrasporangia are also recorded in *Galaxaura* ((342) p. 21), usually occurring on distinct individuals, which commonly differ so markedly in outward form and internal structure from the sexual ones ((51) p. 65, (318), (727) p. 209) that the two phases have in the past been

[1] Skuja ((646) p. 613) questions whether the forms referred by Drew to this species are identical with the widely distributed *A. violaceum*, in which only monospores have hitherto been recorded. Drew's form is certainly identical (178) with the *Chantransia Bowerí* described by Murray and Barton (470).

[2] Kylin ((376) p. 569; cf. also (635) p. 25) has expressed doubts whether the asexual plants, described by Reinke ((539) p. 23) as *Rhodochorton chantransioides* and referred ((368) p. 113, (558) p. 85) to *A. efflorescens*, really belong to this species (cf. however (402) p. 434).

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referred to distinct species.[1] There is perhaps a greater possibility that this advanced member of Nemalionales may be diplobiontic (cf.

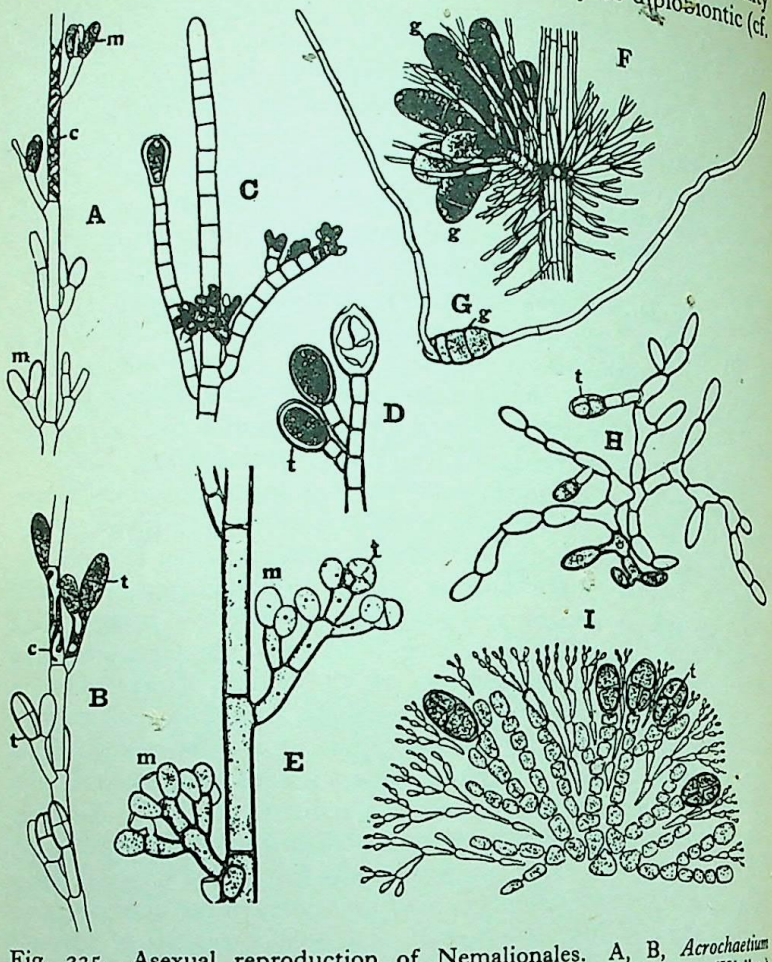

Fig. 235. Asexual reproduction of Nemalionales. A, B, *Acrochaetium efflorescens* (J. Ag.) Naeg. C, D, *Rhodochorton penicilliforme* (Kjellm.) Rosenv., with tetraspores. E, *Acrochaetium violaceum* (Kütz.), monospores and tetraspores. F, G, *Batrachospermum Breutelii* Rabenh.; F, gemma-formation; G, germinating gemma. H, *Rhodochorton membranaceum* Magnus, tetraspore-formation. I, *Liagora tetrasporifera* Boerges., formation of tetraspores in place of carpospores. *c*, chromatophore; *g*, gemma; *m*, monosporangium; *t*, tetrasporangium. (A–D after Rosenvinge; E after Drew; F, G after Skuja; H after Taylor; I after Kylin.)

(347) p. 217), but no conclusion is possible without experimental or cytological verification.

The haplobiontic and diplobiontic Florideae are no doubt related

[1] The record of sporangia with tetrahedral spores on fruiting plants of *G. adriatica* Zan. (cf. (282) p. 307) is open to doubt ((51) p. 76), while the similar record for *Nemalion* ((599) p. 333) may well refer to another organism.

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and many hold that the latter have originated from forms like the Nemalionales with a haplobiontic life-cycle,[1] probably as a sudden mutation ((677) p. 369). Many of the haplobiontic genera show a simple vegetative organisation, but there is nothing to imply a possible reduction from more advanced types. A further discussion of the relation between the haplo- and diplobiontic Florideae is deferred to a later page (p. 736), and the consideration of Nemalionales may be concluded by the mention of a number of instances, which show that the life-cycle may occasionally present interesting complications.

In *Liagora tetrasporifera*, first described ((51) p. 39) from the Canaries, but since found also in the Mediterranean ((389) p. 9), the terminal cells of the gonimoblasts develop as tetrasporangia forming cruciate tetraspores (fig. 235 I, *t*), although most species of *Liagora* produce carposporangia of the usual type. Feldmann ((201) p. 94) has recently recorded a similar formation of cruciate tetrasporangia from the gonimoblasts in *Helminthocladia Hudsoni* (C. Ag.) J. Ag. Should cytological study prove that reduction occurs in the tetrasporangia of these two species, postponement of meiosis within the domain of a single genus would have been demonstrated and a possible stage in the evolution of the diplobiontic condition established.

For members of the Bonnemaisoniaceae Feldmann (198,199) has described the production from the carpospores of an independent generation bearing tetrasporangia. That of *Bonnemaisonia asparagoides* (207) is stated to be identical with a sublittoral alga described by Batters ((29) p. 318; cf. also (225) p. 231, (577) p. 141) as *Hymenoclonium serpens* (*Callithamnion serpens* Crouan), in which the densely branched filaments are creeping and sometimes form an almost continuous expanse; it is to be noted that Crouan's figure shows cruciate tetraspores, whereas Feldmann describes them as tetrahedral. The carpospores of *Asparagopsis armata*, on the other hand, develop into the alga *Falkenbergia* ((198); cf. p. 549) in which hitherto only cruciate tetraspores have been reported ((140) p. 122, (495), (497*a*) p. 136). If these observations are confirmed, they would show that the carpospores of these advanced members of Nemalionales give rise to a generation quite distinct from the sexual one. The fate of the tetraspores is unknown; they may, like the monospores of the juvenile stage of *Batrachospermum*, merely serve to reproduce the generation upon which they occur, while the sexual plant itself arises as an outgrowth from the tetrasporic ones. However that may be, it seems certain that the sexual phase is haploid in view of the data furnished by Svedelius.

Vegetative reproduction is frequent among Nemalionales and occurs abundantly in the "*Chantransia*-stages" of *Batrachospermum* and *Lemanea* (pp. 455, 466); in fragments of *Lemanea*-bristles the longi-

[1] See (167) p. 512, (347) p. 217, (428) p. 682, (671) p. 43, (678) p. 41, (756) p. 435.

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tudinal threads can develop into the "*Chantransia*-stage" ((22) p. 210), while cells of the inner cortex of dead bristles are stated to survive and divide ((72) p. 187). In *Batrachospermum moniliforme* ((650) p. 162) certain laterals, composed of thick-walled cells, have been regarded as resting stages, while in *B. Breutelii* ((642) p. 359) the gonimoblast-threads end in large oval or spindle-shaped bodies (fig. 235 F, *g*) divided by delicate septa into 3–6 cells. In the germination of these propagules (fig. 235 G) the end-cells grow out into threads.

3. The Gelidiales

Earlier researches on the sexual reproduction of these forms ((68) p. 57, (586) p. 228) are supplemented by Kylin's investigation of *Gelidium cartilagineum* ((387) p. 25), upon which the following account is essentially based. The antheridia (cf. also (85) p. 262) form elliptical sori behind the tips of the younger fronds. They are cut off singly from the mother-cells (fig. 236 E, *an*), although a second antheridium is sometimes formed below the first (cf. *Martensia*, p. 701).

In the female plant carpogonia develop just behind the tip within a median fertile tract, which occupies a shallow depression as a result of rapid growth in thickness of the marginal portions of the flat thallus. Later, when formation of carpogonia ceases, the fertile depression comes to lie behind the apex (fig. 236 A, *f*) surrounded by sterile tissue. The fertile tract (fig. 236 B) is occupied throughout its length by an axial plate (*ax*) of large cells, which includes the original axial cells and is extended parallel to the surface. Each cell of the plate (fig. 236 C) cuts off, on either surface of the frond, pericentrals (*p*), many of which give rise to three-celled carpogonial branches (*cp*), in which the two lower cells bear ordinary laterals (*l*) forming the cortex (*co*) of the fertile tract. The clavate trichogyne (*t*) of the carpogonium (*cp*) projects beyond the surface.

The pericentrals also produce small-celled branches (fig. 236 C, *nu*), which form a loose nutritive tissue (fig. 236 G, H, *nu*) around the large cells (*a*) of the axial plate. The entire complex of carpogonia and nutritive tissue, forming the fertile tract, constitutes a *compound procarp* and gives rise to a single fruit; fertilisation of only one of the many carpogonia suffices for further development. A single gonimoblast (fig. 236 D, *g*) arises from the inner side of the fertilised carpogonium, many of its branches (fig. 236 G, *g*) penetrating among the cells of the nutritive tissue (*nu*), which no doubt provides material, although no fusions occur. Other branches of the gonimoblast, more or less perpendicular to the axial complex, bear terminal carposporangia (fig. 236 B, G, *ca*). As development proceeds, the outer cortex (*oc*) of the fertile tract is gradually elevated by elongation of the inner cortical cells (*ic*) so that the mature fruit constitutes a swelling on the frond (cf. fig. 155 A, *cy*). In transverse section it exhibits two imperfectly separated compartments (fig. 236 B), which communicate

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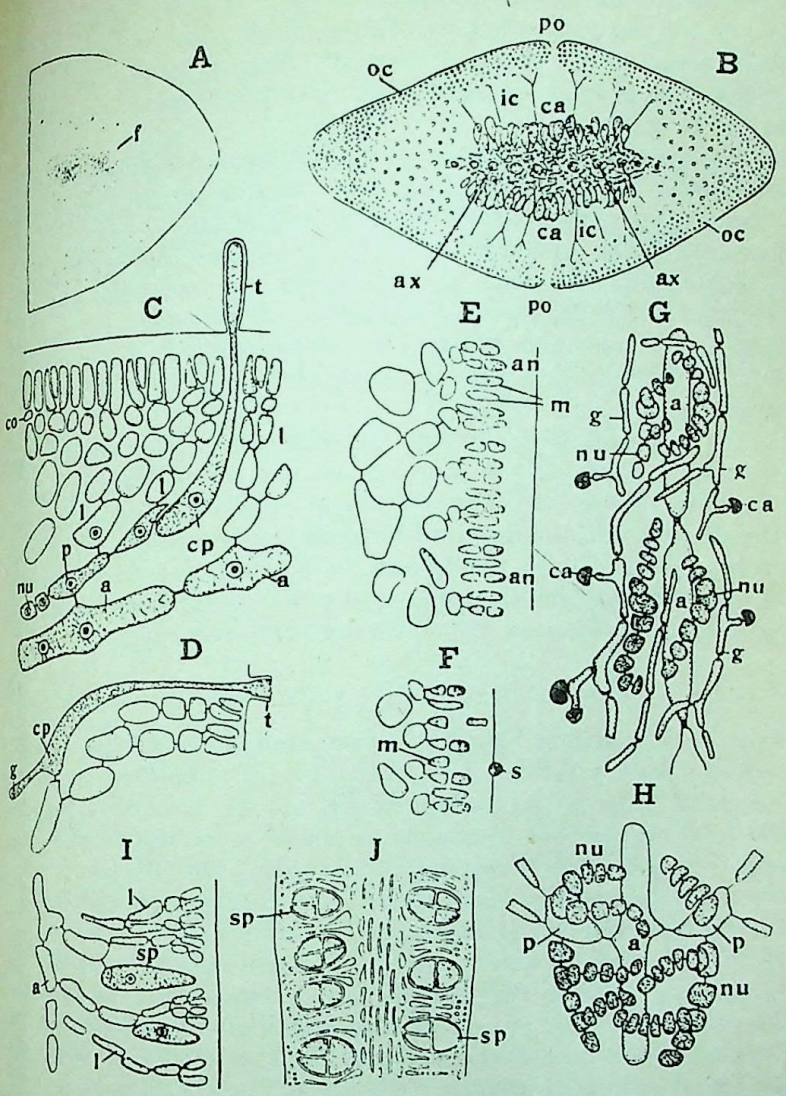

Fig. 236. *Gelidium cartilagineum* Gaill. (after Kylin). A, apex of female frond, with the fertile area (*f*); B, mature fruit in transverse section; C, longitudinal section of frond, with mature carpogonium; D, formation of gonimoblast; E, F, antheridial development; G, gonimoblasts with young carpospores; H, nutritive filaments; I, young sporangium; J, longitudinal section, with mature tetrasporangia. *a*, axial cell; *an*, antheridia; *ax*, axial plate of fertile zone; *ca*, carposporangia; *co*, cortex; *cp*, carpogonium; *g*, gonimoblast; *ic*, inner cortex; *l*, lateral; *m*, antheridial mother-cell; *nu*, nutritive cells or threads; *oc*, outer cortex; *p*, pericentral; *po*, pore; *sp*, tetrasporangium; *t*, trichogyne.

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with the exterior by a median aperture (*po*). In *Pterocladia* ((68) p. 59, (205) p. 96) the fruits are unilateral swellings with a single compartment and a single aperture; here the carposporangia are in short chains. The general course of development appears to resemble that of *Gelidium*.

Tetrasporangia are usually borne on distinct individuals within branches of the fronds that are often dilated and flattened (fig. 155 A, *t*). The sporangia develop from terminal cells of laterals (fig. 236 I, *sp*) and later appear embedded in the surface-tissues (fig. 236 J, *sp*). In *Gelidium* and *Pterocladia* the sporangia are irregularly arranged, while in *Gelidiella*, in which sexual plants are unknown, they are disposed in transverse series. The tetraspores are usually cruciate, but in *Gelidiella* they are frequently tetrahedral ((204) p. 529, (205) p. 94).

The Gelidiales were formerly included among Nemalionales, but were segregated by Kylin ((387) pp. 28, 115) owing to their probable diplobiontic character. The absence of auxiliary cells distinguishes them from other diplobiontic Florideae. The behaviour of the gonimoblast is similar to that found in Naccariaceae, and especially *Naccaria* (p. 616), but the compound procarps and the mode of fruit-development associated with them are very distinctive.

4. The Diplobiontic Type among Cryptonemiales

Like all diplobiontic Florideae, apart from Gelidiales, the Cryptonemiales possess auxiliary cells, which are here sometimes situated at some distance from the carpogonia (fig. 224 A). Connection between the two is established by means of one or more septate, and often branched, *connecting filaments* (*co*). At each point of fusion between the cell of a connecting filament and an auxiliary cell gonimoblasts are usually produced (fig. 240 C, G) and, in certain Cryptonemiales (e.g. *Acrosymphytum*), the same connecting filament can fuse with a number of auxiliary cells, so that a single act of fertilisation results in the formation of several groups of carposporangia (fig. 240 G). In all Cryptonemiales both the carpogonial branches and the auxiliary cells are borne on special accessory laterals and not on those composing the vegetative system.

(*a*) *The Sexual Phase in the non-nemathecial Types*

In *Gloeosiphonia* ((68) p. 42, (389) p. 10, (499) p. 109, (586) p. 230, (634) p. 12) and its allies auxiliary cells and carpogonia are borne on the same branch-system (cf. Endocladiaceae, p. 634), which arises (fig. 237 A, B) from the under side of the basal cell (*b*) of a lateral; all the basal cells of a whorl may be fertile. The three-celled carpogonial branch (*cp*) includes a large hypogynous cell (*hy*) and arises from the first or second cell (*su*) of the fertile axis (*fa*). The fifth cell beyond

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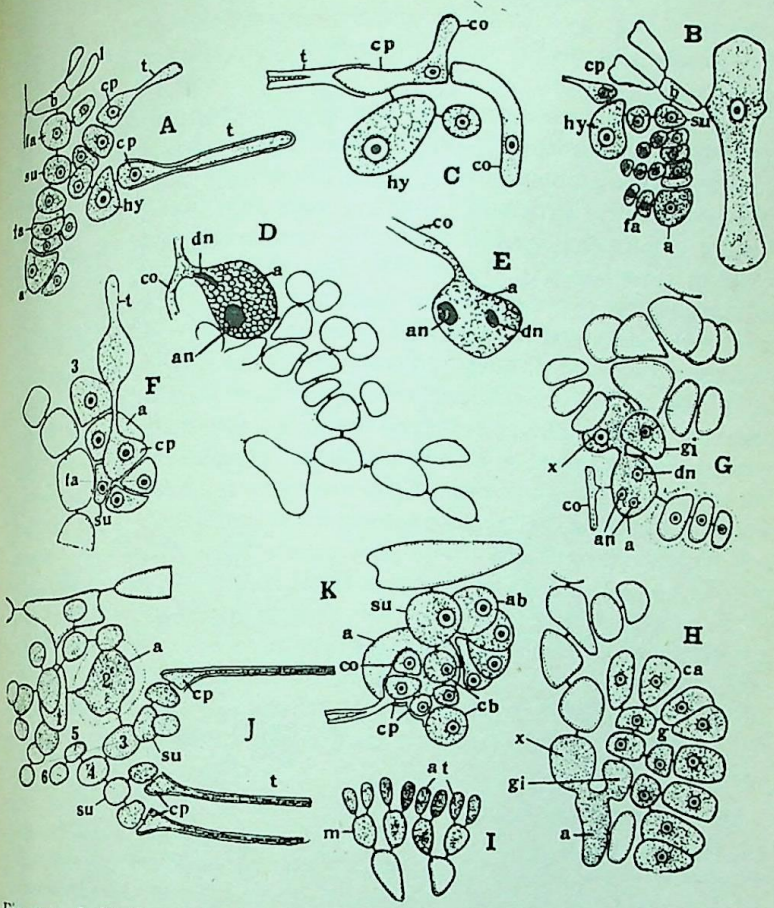

Fig. 237. A–E, G–I, *Gloeosiphonia capillaris* Carm.; A, fertile system with two carpogonial branches; B, ditto with one carpogonial branch; C, development of connecting filaments; D, E, fusion between connecting filament and auxiliary cell; G, the same, formation of gonimoblast-initial (*gi*); H, young gonimoblast; I, antheridia. F, *Thuretella Schousboei* (Thur.) Schmitz, young procarp. J, *Gloeopeltis furcata* (Post. & Rupr.) J. Ag., fertile system with three carpogonial branches and a single auxiliary cell, *1–6* the successive cells of the fertile axis. K, *Schimmelmannia ornata* (Schousb.) Kütz., procarp after fertilisation. *a*, auxiliary cell; *ab*, auxiliary cell branch; *an*, nucleus of auxiliary cell; *at*, antheridia; *b*, basal cell of primary lateral; *cb*, carpogonial branch; *co*, connecting filament; *cp*, carpogonium; *dn*, diploid nucleus; *fa*, fertile axis; *g*, gonimoblast; *gi*, gonimoblast-initial; *hy*, hypogynous cell; *l*, lateral; *m*, antheridial mother-cell; *su*, supporting cell; *t*, trichogyne; *x*, cells of fertile axis that fuse with the auxiliary cell. (D, E after Oltmanns; the rest after Kylin.)

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that bearing the carpogonial branch functions as an intercalary auxiliary cell (*a*), while the rest of the fertile axis is deflected;[1] the cells below the auxiliary cell bear short branches (fig. 237 B). The antheridia (fig. 237 I, *at*) form small superficial sori on the same individuals, the mother-cells (*m*) arising from the tips of the laterals (cf. also (558) p. 278).

The fertilised carpogonium (fig. 237 C) produces two branched connecting filaments (*co*), each containing a product of the zygote-nucleus. They grow in opposite directions towards adjacent auxiliary cells, but do not necessarily connect with that on the same branch-system ((634) p. 14). After fusion the connecting filament may continue to grow (fig. 237 D) towards other auxiliary cells. At the point of contact the membranes are dissolved so that there is free communication between the connecting and auxiliary cells (fig. 237 D, E), and thereupon the diploid nucleus (*dn*) passes into the latter (*a*). As in all diplobiontic Florideae that have been carefully studied, the nucleus of the auxiliary cell (*an*) remains quite distinct and there is nothing of the nature of a nuclear fusion. Soon after (fig. 237 G) both the diploid nucleus and that of the auxiliary cell (*an*) divide. One of the diploid nuclei thereupon passes into an outgrowth of the auxiliary cell which becomes cut off as the gonimoblast-initial (*gi*; "central cell" of Oltmanns), while the other three nuclei (*an*, *dn*) remain in the auxiliary cell. The initial gives rise to a few branching threads (fig. 237 H, *g*), all the cells of which become carposporangia (*ca*). Meanwhile the initial itself (*gi*) fuses with the auxiliary cell (*a*), while the latter fuses with the underlying cell (*x*) of the fertile branch (cf. also fig. 237 G). The carpospores are embedded among the photosynthetic laterals.

In *Thuretella* ((69) p. 185,[2] (284) p. 67, (389) p. 12) the fertile axis (fig. 237 F, *fa*) is reduced, the second cell alone producing a lateral, which consists of three cells. The middle one is the auxiliary cell (*a*), whilst the basal one (*su*) bears the three-celled carpogonial branch, which is bent in such a way that the carpogonium (*cp*) lies adjacent to the auxiliary cell. If the lateral is interpreted as the termination of the fertile axis and the sterile part beyond as a branch, the relative positions of carpogonial branch and auxiliary cell would be similar to those in *Gloeosiphonia*. In *Schimmelmannia* ((389) p. 16) the first (fig. 237 K) or second cell of the fertile axis constitutes the supporting cell (*su*) of the carpogonial branch (*cb*) and bears a further lateral (*ab*) terminated by the auxiliary cell (*a*).

The fertilised carpogonium of *Schimmelmannia* divides transversely (fig. 237 K, *cp*), the upper cell cutting off a connecting cell (*co*) which fuses with the adjacent auxiliary cell (*a*). In *Thuretella* there is no such connecting cell and the carpogonium fuses directly with the auxiliary

[1] Oltmanns regards the auxiliary cell as terminal and the part beyond as a branch.

[2] As *Crouania Schousboei*.

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cell, into which a diploid nucleus passes; a vestige of a connecting cell is perhaps to be found in the occasional division of the carpogonium, one of the resulting cells then fusing with the auxiliary cell. The further

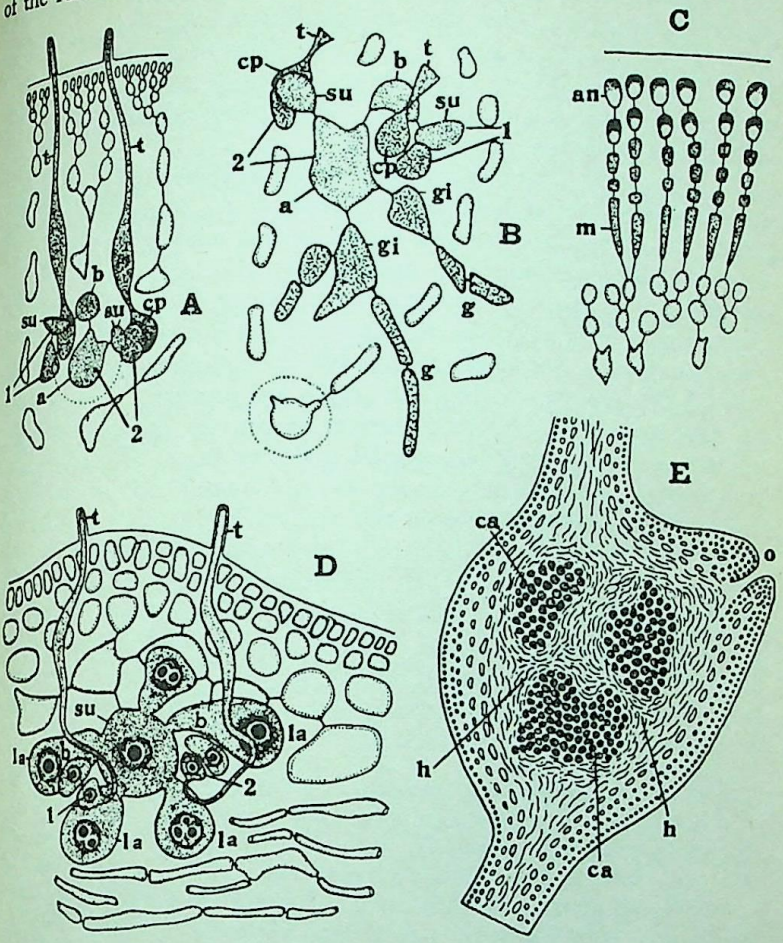

Fig. 238. A–C, *Endocladia muricata* (Post. & Rupr.) J. Ag.; A, mature procarp, with two carpogonial branches (*1*, *2*); B, young gonimoblasts; C, section of antheridial sorus. D, E, *Callymenia reniformis* (Turn.) J. Ag.; D, mature procarp with two carpogonial branches (*1*, *2*); E, ripe fruit. *a*, auxiliary cell; *an*, antheridium; *b*, basal cell of fertile branch; *ca*, carposporangia; *cp*, carpogonium; *g*, gonimoblast; *gi*, gonimoblast-initial; *h*, hyphae; *la*, lateral; *m*, antheridial mother-cell; *o*, aperture of cystocarp; *su*, supporting cell; *t*, trichogyne. (After Kylin.)

development of the gonimoblast in both genera takes place as in *Gloeosiphonia*. In *Thuretella* the groups of carpospores (fig. 152 E, *ca*) become enveloped by threads arising from cells of the fertile lateral.

The close juxtaposition of carpogonium and auxiliary cell in *Thuretella* (fig. 237 F), which warrants the designation *procarp* (p. 601),

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is likewise encountered in the Endocladiaceae (*Endocladia*, fig. 238 A; *Gloeopeltis*, fig. 237 J) and Callymeniaceae (*Callymenia*, fig. 238 D; *Callophyllis*, etc.). The reproductive systems, and particularly that of Callymeniaceae, show distinct resemblances to those of Gigartinales ((387) p. 116, (393) p. 4) and especially of Gigartinaceae. The auxiliary cell is always intercalary. Although the immediate post-fertilisation stages are unknown, connecting filaments are, as in *Thuretella*, probably lacking.

In *Gloeopeltis* ((389) p. 17, (634) p. 9) the auxiliary cell (fig. 237 J, *a*) is one of the lower cells of the fertile axis (*1–6*), while the supporting cells (*su*) of the several two-celled carpogonial branches (*cp*) are laterals. *Gloeosiphonia* also occasionally produces more than one carpogonial branch on the same supporting cell (fig. 237 A). In *Endocladia* (fig. 238 A) the auxiliary cell (*a*) is situated in one of the two carpogonial branches (*1*, *2*), while in *Callymenia reniformis* (fig. 238 D) the large supporting cell (*su*) of the procarp functions also as an auxiliary cell. It bears a number of laterals (*la*), some of which constitute three-celled carpogonial branches (*1*, *2*) with a very large basal cell (*b*), whilst others are represented by this cell alone; there are wide pit-connections between the basal cells and the auxiliary cell. After fertilisation the cells surrounding this procarp of *Callymenia* form numerous hyphae, which constitute a nutritive tissue (fig. 238 E, *h*) into which the branches of the gonimoblast extend. The swollen fruits contain several groups of small carpospores (*ca*) interspersed among the hyphae (cf. Gigartinaceae, p. 672). A definite aperture (*o*) is usually formed in the overlying cortex. These features are found in all Callymeniaceae (cf. also (409)).

The fertile system of *Endocladia* ((387) p. 42) takes the place of one of the accessory branchlets (p. 484) and consists (fig. 238 A) of a basal cell (*b*) bearing two laterals (*1*, *2*), one of which includes the auxiliary cell (*a*). Several gonimoblast-threads (fig. 238 B, *g*) arise from the auxiliary cell after fertilisation and penetrate among the inner cells of the thallus, with which they enter into communication (cf. also (716)). The antheridia (fig. 238 C, *an*) are formed in rows and constitute small irregular sori on the younger parts of the male plants; the elongate mother-cells (*m*) are produced in pairs from the surface-cells.

The above-described procarps of *Callymenia* ((387) p. 59) arise from hypodermal cells which gradually become embedded by division of the superficial cells. In other Callymeniaceae the fertile system is simpler. Thus, in *Callophyllis obtusifolia* ((94) p. 82, (387) p. 57),[1] *Callocolax neglectus* ((29) p. 316, (389) p. 32), and *Euthora cristata* ((389) p. 31) the supporting (auxiliary) cell bears only a single carpogonial branch. According to Kylin the gonimoblast-threads arise from the basal cell of the carpogonial branch in *Callymenia*, although in other Cally-

[1] See also Smith's account (648) of *Callophyllis laciniata* Kütz. (*Rhodymenia laciniata* Grev. (276) pl. 121).

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meniaceae they originate from the auxiliary cell. In *Callophyllis laciniata* the fruits occupy the minute marginal outgrowths of the thallus. The antheridia of Callymeniaceae are imperfectly known.

In diverse Cryptonemiales carpogonia and auxiliary cells are produced on distinct branch-systems, as for instance in the multiaxial Grateloupiaceae. In *Grateloupia filicina* ((39) p. 10, (389) p. 20) these systems (fig. 239 A–C) arise at the boundary between inner and outer cortex and each produces a number of simple laterals (*l*). The two-celled carpogonial branch (fig. 239 A, B, *cp*), the hypogynous cell (*hy*) of which itself bears a lateral (*s*), is borne on one of the lower cells (*su*) of the fertile axis (*1*, *2*), while the large intercalary auxiliary cells (fig. 239 C, *a*) occupy a comparable position. The fertilised carpogonium (fig. 239 F, G) produces several connecting filaments (*co*) which, after fusion with an auxiliary cell (*a*), form a gonimoblast-initial in the same way as in *Gloeosiphonia*. The richly branched gonimoblast bears several distinct groups of carposporangia (so-called *gonimolobes*, fig. 239 E) which are embedded in the thallus; a definite aperture (*o*) is formed in the overlying cortex.

Other Grateloupiaceae differ only in minor respects, although the data are less complete; see Sjöstedt's ((634) pp. 16, 20) investigation of *Cryptonemia borealis* and *Prionitis lanceolata*[1] (fig. 239 D), also *Halymenia* ((39) p. 11, (67) p. 159). In *Cryptonemia* the branches bearing carpogonia and auxiliary cells become surrounded by a loose envelope, which is also indicated in *Grateloupia*. The carpospores seem always to escape through well-defined pores in the cortex.

Comparison of the fertile systems of *Gloeosiphonia* and *Grateloupia* shows that they differ mainly in the segregation of carpogonial branches and auxiliary cells in the latter. The same feature is found in Dumontiaceae, but here the carpogonial branches include special nutritive cells, with which the connecting filaments fuse before they grow onwards to the auxiliary cells proper.

A good illustration is afforded by *Acrosymphytum purpuriferum* (*Dudresnaya purpurifera*, p. 457), which has been repeatedly studied ((67) p. 155, (202) p. 284, (389) p. 22, (499) p. 101, (586) p. 230, (634) p. 8). The carpogonium, which has a long spirally coiled trichogyne (fig. 240 A, C, *t*), is terminal on a colourless accessory branch, arising from the basal cell of a lateral (*b*) and bearing distichous branchlets (*l*). The antheridia are formed in groups from the end-cells of the photosynthetic laterals of the same plant. The fertilised carpogonium usually produces three connecting filaments (fig. 240 C, *co*), which primarily undergo plentiful fusion with cells of the carpogonial branch (fig. 224 A) and especially with the end-cells (*n*) of the laterals; these possess dense contents and constitute nutritive cells (sterile

[1] Cf. also the account of Daines ((150) p. 289) which is, however, incorrect in certain important particulars.

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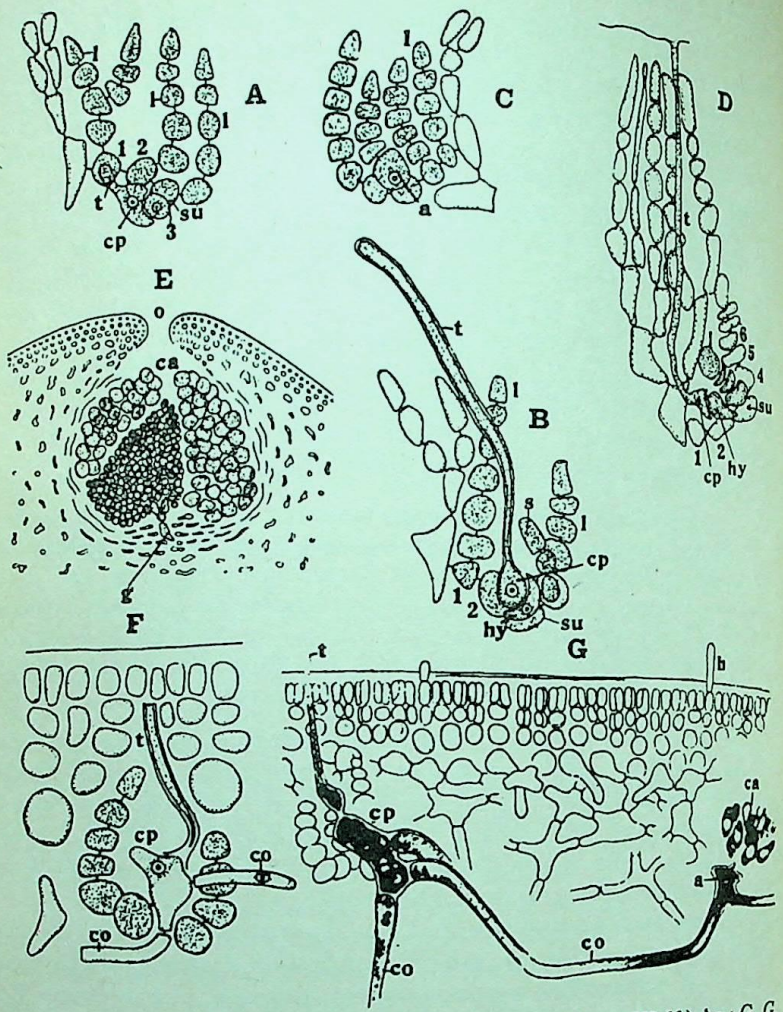

Fig. 239. A–C, E–G, *Grateloupia*; A–C, E, F, *G. filicina* (Wulf.) Ag.; G, *G. dichotoma* J. G. Ag. A, young and B, mature carpogonial systems, *1–3* successive cells of axis; C, fertile system with auxiliary cell (*a*); E, fruit and ripe carpogonial system, *1–6* successive cells of axis. *a*, auxiliary cell; *ca*, carposporangium; *co*, connecting filament; *cp*, carpogonium; *g*, gonimoblast; *h*, hair; *hy*, hypogynous cell; *l*, lateral; *o*, aperture of fruit; *s*, sterile thread; *su*, supporting cell; *t*, trichogyne. (D after Sjöstedt; G after Berthold; the rest after Kylin.)

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auxiliary cells of Berthold (39) p. 14). Subsequently the connecting filaments penetrate for considerable distances among the vegetative laterals until, probably as a result of a chemotropic stimulus, they make contact with an auxiliary cell (fig. 240 C, *). The auxiliary cells, which are distinguished by dense contents and scanty pigmentation, terminate unbranched accessory laterals (fig. 240 B, *a*), arising in the

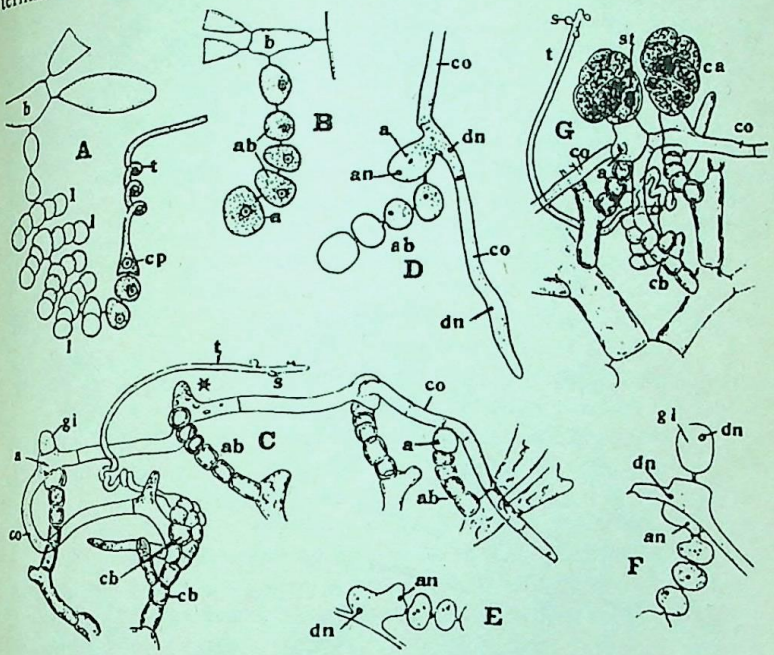

Fig. 240. *Acrosymphytum purpuriferum* (J. Ag.) Kyl. A, carpogonial branch; B, auxiliary cell branch; C–F, fusion of connecting filaments with auxiliary cells and formation of gonimoblast-initial; G, two mature gonimoblasts. *a*, auxiliary cell; *ab*, auxiliary cell branch; *an*, auxiliary cell nucleus; *b*, basal cell of primary lateral; *ca*, carposporangia; *cb*, carpogonial branch; *co*, connecting filament; *cp*, carpogonium; *dn*, diploid nucleus; *gi*, gonimoblast-initial; *l*, lateral; *s*, spermatium; *st*, sterile cell of gonimoblast; *t*, trichogyne; * (in C), point of fusion between connecting filament and auxiliary cell. (A, B, D after Kylin; C, E, F after Oltmanns; G after Bornet & Thuret.)

same position as the carpogonial branches, but more numerous than the latter (cf. fig. 240 C).

Contact between connecting filament and auxiliary cell is followed in the usual way by the establishment of cytoplasmic continuity (fig. 240 D). Here, however, the connecting cell gives rise to the gonimoblast-initial (fig. 240 C, F, *gi*) which is cut off on the side opposite to the auxiliary cell; successive stages are shown diagrammatically in fig. 224 B, D, and C. The gonimoblast-initial produces a compact group of branches (fig. 240 G) and all the cells except for the basal one (*st*) produce carpospores. Meanwhile the connecting filament

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continues its growth towards other auxiliary cells (fig. 240 C), a septum separating the fusing portion from the growing tip beyond.

A comparable method of carpospore-formation is met with in other Dumontiaceae. Details are available for *Dudresnaya coccinea*[1] ((67) p. 158, (68) p. 35, (387) p. 32, (499) p. 106), *Dumontia incrassata* ((183) p. 440, (380) p. 11, (492) p. 65, (558) p. 157, (586) p. 230), *Thuretellopsis*[2] ((383) p. 14), *Cryptosiphonia Woodii* ((389) p. 24, (634) p. 4) and *Dilsea*

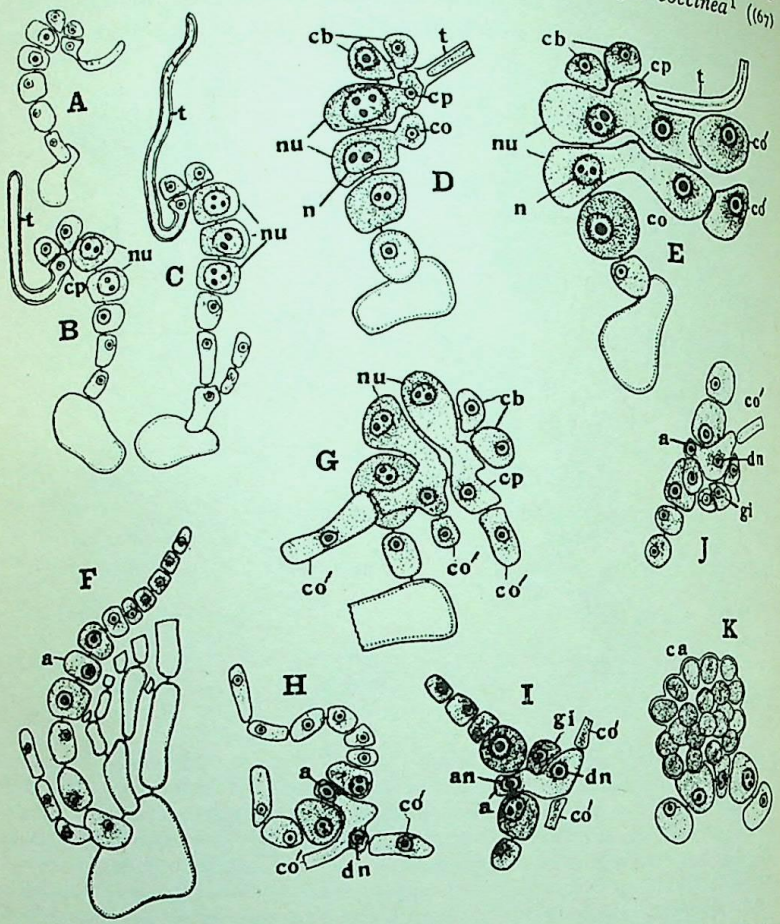

Fig. 241. *Dudresnaya coccinea* (Ag.) Crouan (after Kylin). A, young carpogonial branch; B, C, mature carpogonial branches; D, fusion of connecting cells with nutritive cells; E, G, origin of secondary connecting filaments (*co′*); F, auxiliary cell branch; H, fusion between connecting filament and auxiliary cell; I, J, formation of gonimoblast-initials (*gi*); K, young gonimoblast. *a*, auxiliary cell; *an*, auxiliary cell nucleus; *cb*, carpogonial branch; *co*, primary and *co′*, secondary connecting filaments; *cp*, carpogonium; *dn*, diploid nucleus; *gi*, gonimoblast-initial; *n*, nucleus; *nu*, nutritive cells; *t*, trichogyne.

[1] Cf. also *D. crassa* ((314) p. 572).

[2] Vegetatively just like *Thuretella*.

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edulis ((554) p. 20, (558) p. 160). The branches bearing auxiliary cells are always more numerous than those with carpogonia, and both usually originate from the basal cells of the laterals; they exhibit little or no branching (figs. 241 A–C, F; 243 A). In *Dumontia* (fig. 242 A, B) they arise from the cells composing the longitudinal branches of the primary laterals. A difference from *Acrosymphytum* is constituted by the intercalary position of the nutritive cells within the carpogonial branches (figs. 241 B, C; 242 D; 243 A, *nu*). The latter are curved in such a way that the carpogonium (*cp*) lies close to the cells in question. The auxiliary cells occupy a similar intercalary position, although their exact location varies (cf. figs. 241 F, *a*; 242 F, *ax*).

In *Dudresnaya* the fertilised carpogonium divides to form a two-celled connecting filament (fig. 241 D, *co*) which fuses with the adjacent nutritive cells (*nu*). Most of the cytoplasm accumulates in the connecting cells (fig. 241 E), which soon give rise to longer filaments (fig. 241 E, G, *co'*). In *Dumontia* (fig. 242 B) the carpogonium (*cp*) usually fuses with the third cell (*nu*) of its branch, although more than one cell (fig. 242 E, *fu*) may be involved ((558) p. 157); two or three connecting filaments (fig. 242 D, E, *co*) then arise from the nutritive cell. Much the same occurs in *Cryptosiphonia* (fig. 243 B) and *Thuretellopsis*.

Both in *Dudresnaya* and *Dumontia* the auxiliary cell develops a short process, which fuses with the connecting filament and receives a diploid nucleus from it (fig. 241 H). Two or three gonimoblast-initials (figs. 241 I, J, *gi*; 242 F) are cut off from this process, i.e. from the auxiliary cell. The connecting filaments for the most part seek out a number of successive auxiliary cells, but this is stated to be unusual in *Dumontia*. As in *Acrosymphytum*, most of the cells of the gonimoblast-threads produce carpospores (figs. 241 K; 242 F). No protective envelope is organised, the carpospores lying embedded in slight swellings on the thallus.

The male plants of *Dudresnaya* (cf. also (85) p. 259) and *Dumontia* ((183) p. 437, (258) p. 233, (558) p. 157) are smaller than the female, and in *Dumontia* almost the entire surface may become fertile. Each mother-cell (fig. 242 G, *m*) produces successively three antheridia (*a*).

In Grateloupiaceae and Dumontiaceae the branches bearing carpogonia and auxiliary cells respectively are clearly homologous, and in Dumontiaceae the nutritive and auxiliary cells occupy comparable positions within them. There is also considerable similarity with *Gloeosiphonia*, and the two families under discussion could be regarded as divergent evolutionary series from a generalised type possessing carpogonia and auxiliary cells on the same branch-system. In Grateloupiaceae (cf. (387) p. 116) complete separation of the two structures has taken place, while in Dumontiaceae auxiliary cells still persist in the carpogonial branches and function as nutritive cells. From this point of view Berthold's designation of them as "sterile auxiliary cells" is quite apposite. It is also noteworthy that in *Dumontia* ((380) p. 12) the auxiliary cell branches lack the terminal cell which, on the carpogonial branches, develops into the female organ.

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In support of the view that a type comparable to *Gloeosiphonia* may have constituted the starting-point for the evolution of these two series, it may be recalled that the cells functioning as auxiliary cells in

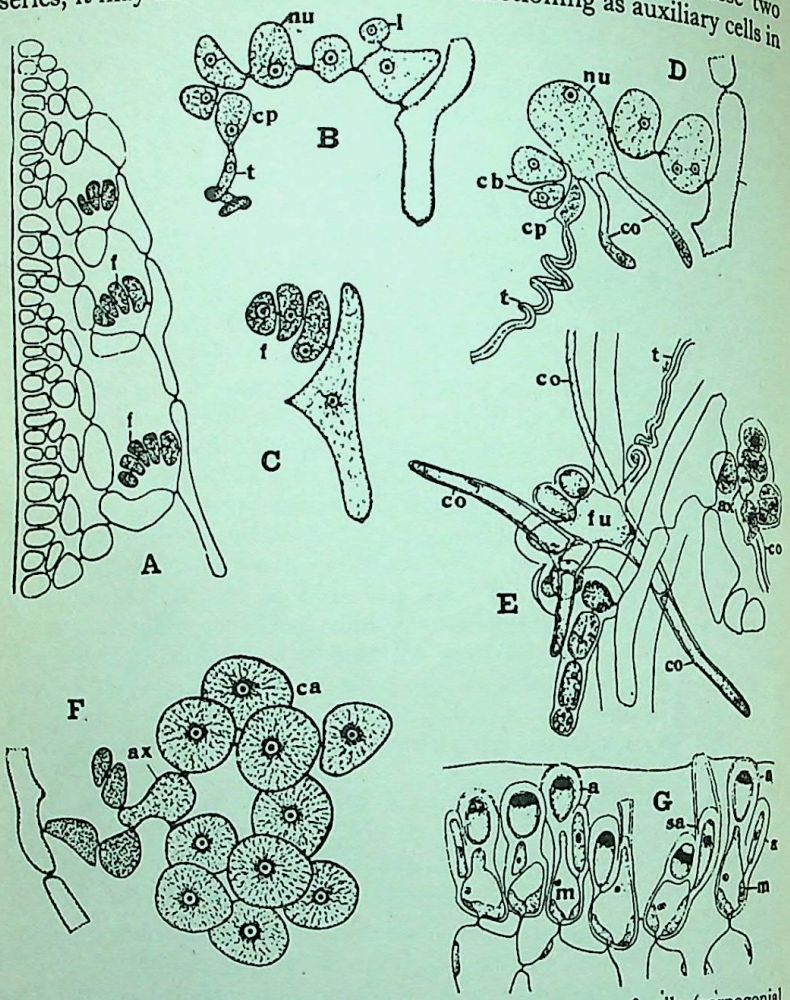

Fig. 242. *Dumontia incrassata* Lamour. A, three young fertile (carpogonial or auxiliary) branches in longitudinal section of thallus; B, mature carpogonial branch; C, young fertile branch; D, formation of connecting filaments (somewhat diagrammatic); E, the same; F, mature gonimoblast; G, antheridial development. *a*, antheridium; *ax*, auxiliary cell; *ca*, carposporangia; *cb*, carpogonial branch; *co*, connecting filament; *cp*, carpogonium; *f*, fertile (accessory) branches; *fu*, fusion-cell; *l*, lateral; *m*, antheridial mother-cell; *nu*, nutritive cells; *sa*, secondary antheridium; *t*, trichogyne. (E after Rosenvinge; G after Grubb; the rest after Kylin.)

some of the advanced haplobiontic forms invariably occur in an intercalary position in the carpogonial branch (cf. also (678) p. 47).

In the genera above considered the diploid nucleus from the connecting filament usually passes into the auxiliary cell, and, as in most

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diplobiontic Florideae, it is from the latter that the gonimoblast-initials are formed. *Acrosymphytum* is exceptional in that the initial is formed from the connecting filament (fig. 240 F, G), within which the diploid nucleus (*dn*) remains after fusion with the auxiliary cell. An analogous condition is seen in *Cruoria* and *Petrocelis* (Cruoriaceae), although here (fig. 243 G) the initials (*gi*) do not arise at the point of fusion with an auxiliary cell. Kylin ((387) p. 115, (389) p. 98) regards

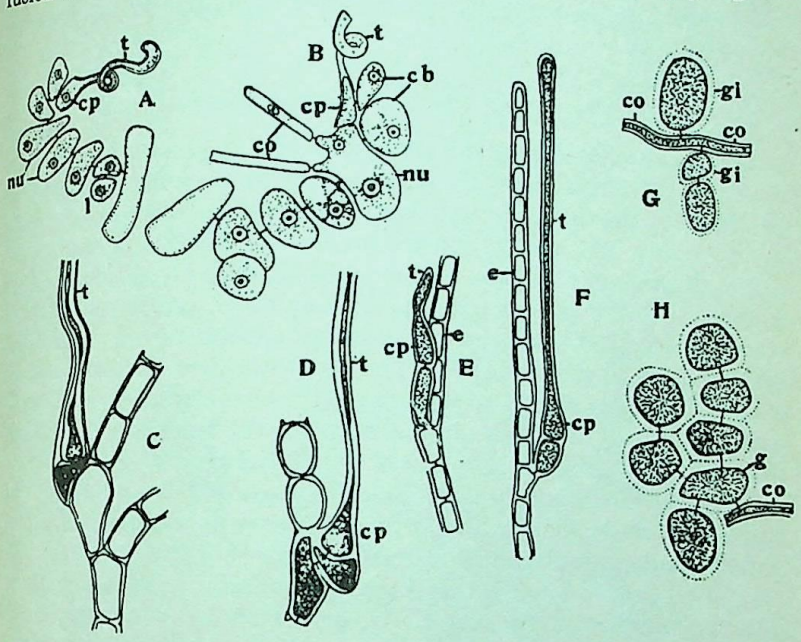

Fig. 243. A, B, *Cryptosiphonia Woodii* J. Ag.; A, carpogonial branch; B, formation of connecting filaments. C, D, *Petrocelis Hennedyi* (Harv.) Batt., carpogonial branches. E–H, *Cruoria pellita* (Lyngb.) Fries; E, young and F, mature carpogonial branches; G, formation of gonimoblast-initials (*gi*); H, mature gonimoblast. *cb*, carpogonial branch; *co*, connecting filament; *cp*, carpogonium; *e*, erect thread of crust; *g*, gonimoblast; *gi*, gonimoblast-initial; *l*, lateral; *nu*, nutritive cells; *t*, trichogyne. (C, D after Rosenvinge; the rest after Kylin.)

these genera as primitive,[1] but their vegetative structure does not lend support to such a view and there is little in their reproduction to favour it. They are just as likely to be specialised forms.

In *Cruoria pellita* ((387) p. 31, (558) p. 182) the 2–3-celled carpogonial branches (fig. 243 E, F) are borne on a lower cell of an erect thread (*e*). The thick connecting filaments (fig. 243 G, H, *co*) extend parallel to the surface of the crust and fuse with certain little differentiated middle

[1] Kylin ((393) p. 76) at one time regarded the Cruoriaceae as the lowest members of Gigartinales, but he appears since ((400) p. 217) to have abandoned this view.

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cells of the erect threads. The gonimoblast-initials (fig. 243 G, *gi*) arise from diverse points on the outer or inner sides of the connecting filaments and develop into little-branched threads (fig. 243 H, *g*) in which all the cells become carposporangia.

Petrocelis Hennedyi ((558) p. 177, (586) p. 230) has similar carpogonial branches (fig. 242 C, D) and here the cells with which the connecting filaments fuse are somewhat swollen and stain readily. The antheridia in both genera ((558) pp. 177, 182) are produced at the tips of one- (rarely two-) celled branchlets arising from the upper cells of the erect threads.

(*b*) *The Sexual Phase in the Nemathecial Types*

In the Rhizophyllidaceae and Squamariaceae the fertile branches are confined to special *nemathecia* which form irregular cushion-like swellings on the thalli (fig. 178 A, *n*). Those of *Polyides rotundus* ((380) p. 17, (586) p. 230, (692) p. 77) are found upon the younger branches in late summer and autumn and are shed after the escape of the spores ((558) p. 173). In section (fig. 244 A) they show a dense aggregate of sterile and fertile threads, which grow out vertically from the surface-cells of the thallus (fig. 244 H). The little-branched sterile threads (*s*) overtop the unbranched fertile ones (*f*), which terminate in a carpogonium (*cp*) cut off by an oblique septum; the spirally coiled trichogyne (*t*) alone projects beyond the surface of the nemathecium.

The post-fertilisation stages resemble those of Dumontiaceae. The single connecting filament, after fusing with certain cells of the carpogonial branch, gives rise to several secondary filaments (fig. 244 D, *co*) which ramify among the threads composing the nemathecium. The auxiliary cells (fig. 244 C, D, *a*), which are intercalary in the sterile threads, develop a lateral process (*p*), with which the tip of a connecting filament fuses; subsequently the latter may continue its growth. The gonimoblast (fig. 244 C, *g*), which arises from the connecting filament (cf. *Acrosymphytum*), bears short, densely packed branches forming carposporangia (*ca*) terminally, and each nemathecium contains a considerable number of these sporogenous groups (fig. 244 D). In *Rhizophyllis* only mature nemathecia are so far known.

The male nemathecia of *Polyides* appear as small white cushions ((380) p. 19, (586) p. 233, (692) p. 76) composed of colourless threads (fig. 244 G), in which the upper cells cut off 2–4 pericentrals constituting mother-cells (*m*); each generally produces three antheridia (*an*).

In *Peyssonnelia* ((383) p. 27, (387) p. 35, (558) p. 194, (586) p. 232) the fertile threads (fig. 244 B, *f*) are laterals on the lowest cell of the sterile threads (*s*) composing the nemathecium. The carpogonium (*cp*) is cut off obliquely so that its lower end is adjacent to the hypogynous (nutritive, *nu*) cell with which it fuses after fertilisation. The connecting filament (fig. 244 F, *co*) grows more or less horizontally towards the

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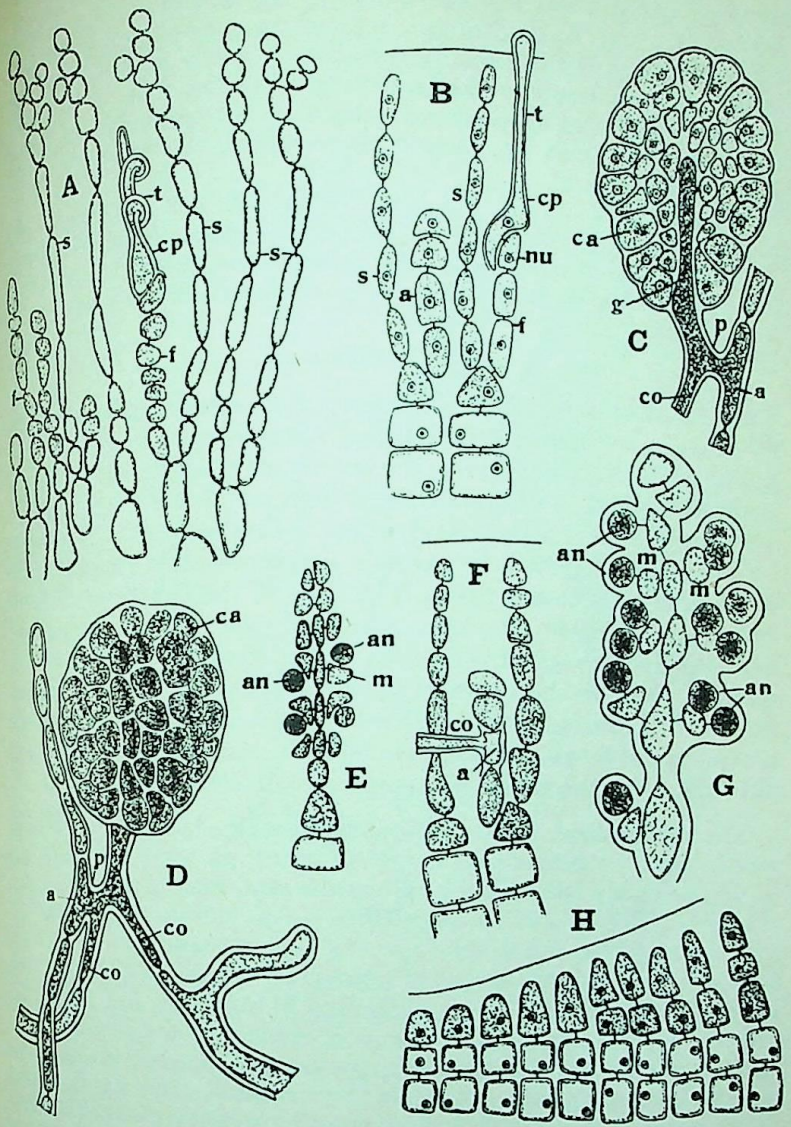

Fig. 244. A, C, D, G, *Polyides rotundus* (Gmel.) Grev.; A, vertical section of nemathecium, with two fertile branches (*f*); C, gonimoblast in section; D, ditto, from the surface; G, antheridial development. B, E, F, H, *Peyssonnelia Dubyi* Crouan; B, vertical section of nemathecium with carpogonial and auxiliary cell branches; E, antheridial development; F, fusion between connecting filament and auxiliary cell; H, early development of nemathecial threads (shaded). *a*, auxiliary cell; *an*, antheridium; *ca*, carposporangia; *co*, connecting filament; *cp*, carpogonium; *f*, fertile thread of nemathecium; *g*, gonimoblast; *m*, antheridial mother-cell; *nu*, nutritive cell; *p*, process of auxiliary cell; *s*, sterile thread of nemathecium; *t*, trichogyne. (After Kylin.)

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auxiliary cell (*a*), which is constituted by the second lowest cell of its branch (fig. 244 B, *a*). The few cells of the gonimoblast all become carposporangia and the mature nemathecia usually contain numerous groups of carpospores. The antheridial branches ((358) p. 393, (558) p. 194) either occur in special nemathecia or interspersed in the female ones; the antheridia are formed in essentially the same way as in *Polyides* (fig. 244 E).

Cruoriopsis ((31) p. 388, (53) p. 11, (202) p. 298, (558) p. 184, (584), (727) p. 262; incl. *Plagiospora* ((358) p. 593) differs chiefly from *Peyssonnelia* in the absence of nemathecia, the diverse reproductive organs being borne terminally or laterally on the erect threads of the crust.

(*c*) *Corallinaceae*

The Corallinaceae exhibit specialisation in sexual reproduction, no less than in vegetative organisation. Except in the uncertain endophytic genus *Schmitziella* (28), the sex organs are invariably produced within conceptacles of diverse shape (figs. 245 I; 246; 247 A), which are either sunk in the thallus or project to a marked extent. They arise by the arrest of growth in a certain region which is gradually overarched by the adjacent tissue. The floor of the conceptacle, constituting the so-called *disc*, thus represents the original surface-layer and usually consists of cells with dense contents. It is these that divide to form the short vertical threads, upon which the sex organs are produced. The conceptacle is therefore a nemathecium which is overgrown by the surrounding tissue. Many Corallinaceae are dioecious, although *Corallina rubens* and some *Melobesias* are monoecious.

The development of the conceptacles, described in detail in *Corallina mediterranea* by Solms-Laubach ((652) p. 32; cf. also (659) p. 31, (692) p. 94), probably takes place in much the same way in other species of the genus. The apex of the segment broadens and the layer of thickening covering the apical cells (p. 474) is thus disorganised. This is followed by the development of a marginal upgrowth (fig. 250 A, *tc*), which gradually bends inwards (fig. 250 B) until only a small aperture remains (fig. 245 I). During the development of the conceptacle the outer walls of the elongate cells composing the disc (fig. 250 A, *d*) become strongly thickened, while the outermost layers (*pr*) undergo calcification so that the floor is covered by a continuous layer of lime, separated from the underlying cells by a stratum of mucilage (*m*). The latter gradually increases in amount, thus raising the layer of lime (fig. 250 B) and ultimately causing its rupture.

The raised conceptacles of *Melobesia* occupy parts of the crust which consist of several layers of cells. In *M. limitata* ((659) p. 15) and others the disc is constituted by the second layer (fig. 246 A, G, *d*) and, as these cells divide to form the fertile threads (*f*), the cover-cells (*c*) are carried up and gradually cast off; the lid of the conceptacle is formed by division and elongation of the surrounding cells. Much the same occurs in *Lithophyllum* and *Lithothamnion*. The broad and often completely em-

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bedded conceptacles of the former (cf. fig. 250 G) have an elongate canal-like aperture, sometimes lined with hairs ((215) p. 16, (415) p. 56, (482) p. 349, (652) p. 61, (659) p. 22); those of *Lithothamnion* are usually

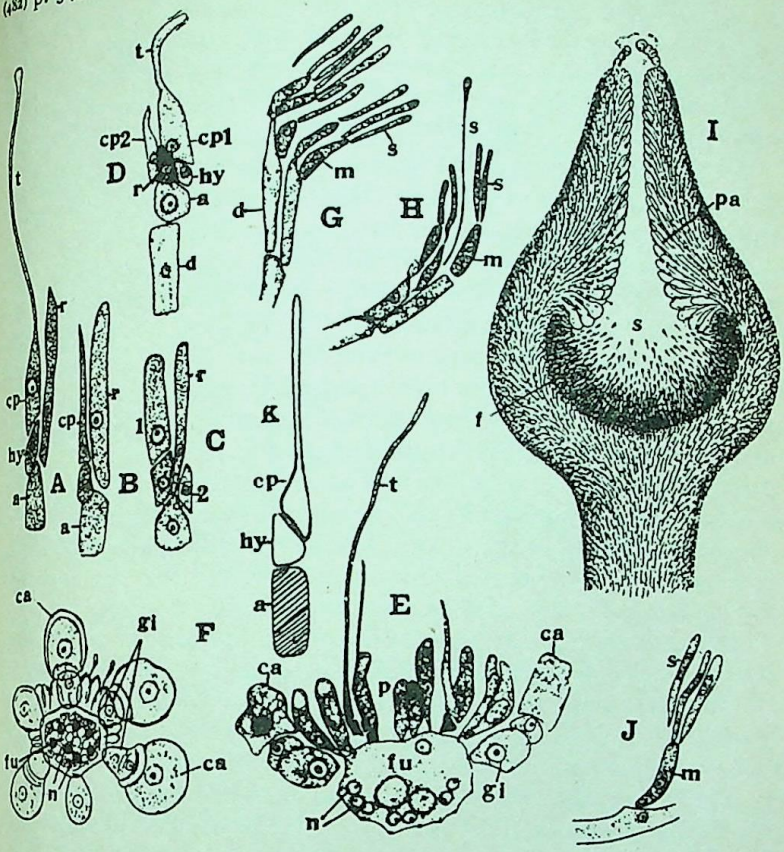

Fig. 245. *Corallina*; E, *C. rubens* Ellis & Soland.; F, *C. virgata* Zanard.; I, *C. mediterranea* Aresch.; the others *C. officinalis* L. A–D, diverse developments of procarps; E, fusion-cell (*fu*) in vertical section, with carposporangia and remains of procarps; F, the same from the surface; G, H, J, antheridial development; I, vertical section of male conceptacle; K, diagram of simplest type of procarp found in *Corallina*. *a*, auxiliary cell; *ca*, carposporangia; *cp*, carpogonium; *d*, disc-cell; *f*, fertile layer in male conceptacle; *fu*, fusion-cell; *gi*, gonimoblast-initial; *hy*, hypogynous cell; *m*, antheridial mother-cell; *n*, nuclei; *p*, remains of procarps; *pa*, paraphyses; *r*, rudiment of carpogonial branch; *s*, spermatium; *t*, trichogyne. (F after Solms-Laubach; I after Thuret & Bornet; the rest after Suneson.)

markedly raised ((215) p. 10, (415) p. 54, (659) p. 64). The male conceptacles of *Melobesia* and *Lithophyllum* are smaller than the female and the aperture is often prolonged into a mucilage-tube ((558) p. 242, (659) p. 11, (720) p. 367). In *Epilithon* ((387) p. 37, (659) p. 60) the fertile threads are formed by division of the cells of the basal stratum (fig. 246 C, D,

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F, *b*) and, as they develop (*f*), the strongly calcified superjacent layers (*u*) are thrown off. The conceptacles of *Choreonema* (p. 582) first appear within the cortex of the host as fan-shaped groups of threads (fig. 247 A, *co*) terminal on one of the endophytic filaments ((455), (652) p. 54, (692) p. 98), the end-cells being provided with mucilaginous caps. The wall of the conceptacle is largely formed by tabular cells (*c*) cut off tangentially from the peripheral threads, although near the aperture some of the inner threads (*i*) are involved.

In the female conceptacles ((659) p. 76) the fertile threads (fig. 246 A, F, *f*) are confined to the floor. The cells of the disc (*d*) divide and the upper half produces the procarp (fig. 245 D); occasionally two or more procarp rudiments are formed from a single disc-cell. The development of the numerous procarps takes place centrifugally, but as a rule only the central ones mature (fig. 246 A, F). The trichogynes are usually elongate and project from the aperture of the conceptacle (figs. 246 A; 247 A). Recent investigations ((387), (455), (659); cf. also (586) p. 234)[1] indicate that the basic type of procarp in Corallinaceae (fig. 246 H) consists of a basal (auxiliary) cell (*a*) bearing two 2-celled carpogonial branches (*1*, *2*), as well as an imperfect median rudiment (*r*); the nearest approach to this is found in some *Melobesias* and in *Amphiroa rigida* ((659) pp. 9, 49). One of the carpogonial branches is, however, often represented only by a single cell (fig. 246 I) or, like the median rudiment, may be completely suppressed (fig. 245 K).

The auxiliary cell may likewise bear three branches in *Lithophyllum expansum* ((659) p. 22) and *Corallina* ((652) p. 39,[2] (659) p. 31; fig. 245 C, D), but here only one (*cp1*) develops into a complete carpogonial branch, while one (fig. 245 A, B) or both of the others (cf. fig. 245 K) may be suppressed. The last condition is typical of *Choreonema* ((455) p. 12) (fig. 247 B), where the single two-celled carpogonial branch (*cp*) surmounts an auxiliary cell (*a*), the tip of which is produced and, like the median rudiment in the other types, lies adjacent to the carpogonium. In the procarps of *Lithothamnion* ((482) p. 345, (659) p. 64) and *Epilithon* ((387) p. 37) this protrusion is lacking so that the auxiliary cell appears as the basal cell of a three-celled carpogonial branch (fig. 245 K). The preceding account is based on that of Suneson (659), who interprets the diverse stages as a reduction series.

In *Choreonema* (fig. 247 A) all the procarps of a conceptacle are fully differentiated, but in *Corallina* the carpogonial branches in the marginal procarps remain unicellular and in *Lithothamnion* and

[1] For occasional data, see also (295) p. 13, (297) p. 70, (303) p. 226, (558) pp. 214, 230. The peculiar statements of Heydrich (298, 304) regarding the post-fertilisation stages in *Lithophyllum* and *Lithothamnion*, which are summarised by Pilger ((526) p. 261), have never been corroborated (cf. (659) p. 80). Many of Heydrich's observations are erroneous.

[2] Solms-Laubach's interpretation is scarcely borne out by his figures (cf. (455) p. 16). Yamanouchi's ((757) p. 94) account of *C. mediterranea* is also at variance with recent observations.

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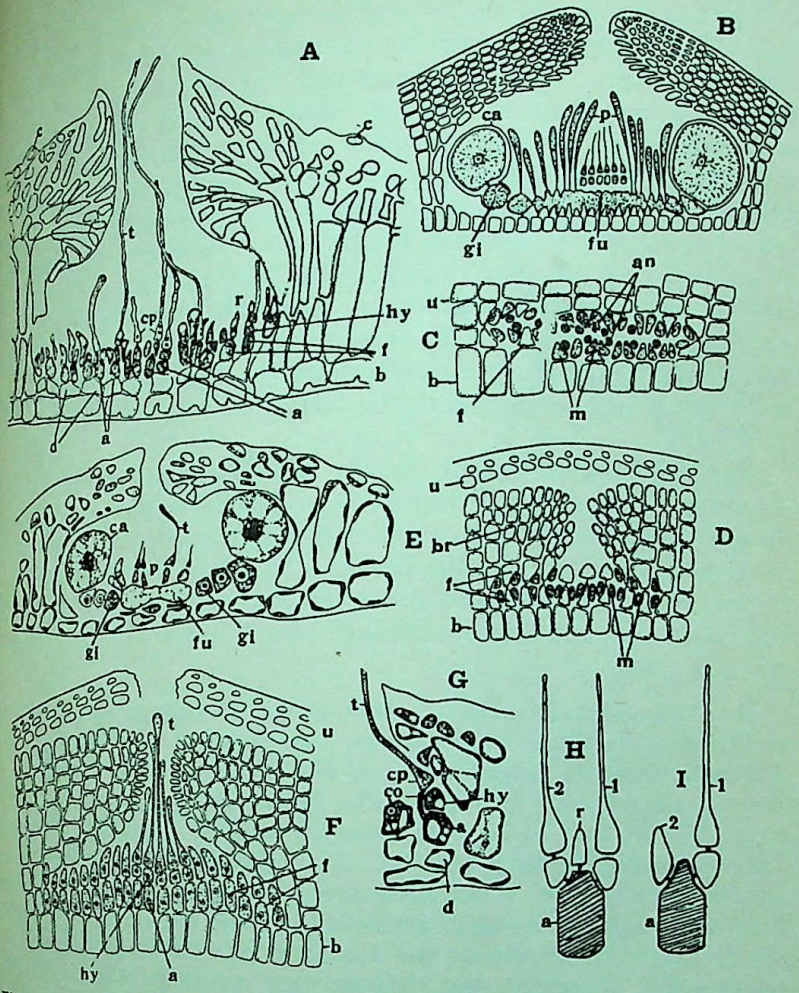

Fig. 246. A, E, G, *Melobesia*; A, *M. limitata* (Fosl.) Rosenv.; E, G, *M. Lejolisii* Rosanoff. A, vertical section of mature female conceptacle; E, ditto, after formation of fusion-cell and carposporangia; G, formation of connecting filament (*co*) between carpogonium and auxiliary cell. B–D, F, *Epilithon membranaceum* (Esper.) Heydr.; B, vertical section of female conceptacle, with fusion-cell and mature carposporangia; C, excentric vertical section of male conceptacle; D, median section of same; F, vertical section of female conceptacle, with mature carpogonia. H, I, diagrams representing the basic (H) and a derived (I) type of procarp. *a*, auxiliary cell; *an*, antheridia; *b*, basal layer of thallus; *br*, sterile branches; *c*, cover-cell; *ca*, carposporangia; *co*, connecting filament; *cp*, carpogonium; *d*, disc-cells; *f*, fertile threads; *fu*, fusion-cell; *gi*, gonimoblast-initial; *hy*, hypogynous cell; *m*, antheridial mother-cell; *p*, remains of procarps; *r*, rudiment of carpogonial branch; *t*, trichogyne; *u*, roof of conceptacle. (B–D, F after Kylin; the rest after Suneson.)

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Epilithon (fig. 246 F) two-celled. Fertilisation of a single carpogonium suffices for further development. The subsequent events are difficult to follow. In *Melobesia* Suneson ((659) p. 10) observed (fig. 246 G) the outgrowth from the carpogonium (*cp*) of a short connecting filament (*co*) which fused with the auxiliary cell (*a*) of the same procarp; this may well represent the usual course of events, although fusion with some other adjacent auxiliary cell is also possible. After the passage of the diploid nucleus into an auxiliary cell, all the auxiliary cells of a conceptacle undergo progressive fusion ((652) p. 43), which results in the formation of a large multinucleate fusion-cell (figs. 245 E, F; 246 B, E, *fu*) bearing on its upper side the remains (*p*) of the diverse procarps. Some of the nuclei in this cell are commonly larger (fig. 245 E) or richer in chromatin ((757) p. 95) and are probably diploid. In *Lithothamnion* the layer below the auxiliary cells also seems to enter into the formation of the fusion-cell ((659) p. 66).

The gonimoblast-initials usually arise from the margin of the fusion-cell (figs. 245 E, F; 246 B, E, *gi*) and develop into unbranched threads, which form large uninucleate carposporangia (*ca*) in basipetal sequence. In certain species (*Melobesia limitata*, *Amphiroa rigida*) gonimoblast-threads also originate from the upper surface of the fusion-cell, and this is sometimes also so in *Corallina* (cf. also (558) pp. 214, 273).

In *Choreonema* ((455) p. 17, (659) p. 55) the stages subsequent to fertilisation are somewhat different. The carpogonium (fig. 247 C, *cp*) enlarges, while its hypogynous cell (*h1* in fig. 247 D) persists longer than in the adjacent procarps. The female organ (*1*) fuses with the auxiliary cell (*a1*) of its own procarp, but the diploid nucleus (*dn*) remains within the carpogonium. After this the latter puts out short connecting processes, which successively fuse with slight protuberances from the neighbouring auxiliary cells (*a2*), and by degrees (fig. 247 E) all the latter are involved; the auxiliary cells finally degenerate. In *Choreonema*, therefore, the carpogonium progressively absorbs the contents of the auxiliary cells and ultimately appears as a large lobed cell (fig. 247 F), containing a number of diploid nuclei; this forms the basipetal rows of carposporangia in the usual way.

In the male conceptacles the fertile threads either occupy the floor only (*Melobesia*, *Lithophyllum*, *Amphiroa*) or also spread on to the side-walls (*Corallina*, fig. 245 I, *f*; *Choreonema*; *Epilithon*; *Lithothamnion*) (cf. (760) p. 120); in *Corallina* the part of the wall near the aperture is covered with sterile paraphyses (*pa*). The details of antheridial development are difficult to decipher, but as a general rule the cells of the disc seem to cut off two (sometimes perhaps more) elongate mother-cells[1] (fig. 245 G, *m*), which form a dense layer ((558) pp. 242,

[1] The mother-cells in *Lithothamnion Lenormandi* are stated to be formed from systems of branched threads ((297) p. 65, (558) p. 218).

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267, (659) p. 82, (757) p. 93); each mother-cell produces apically a number of, often elongate, antheridia (fig. 245 G, J, *s*). There is considerable evidence that the entire antheridium functions as the spermatium ((652) p. 37, (659) p. 83). At the time of detachment (fig.

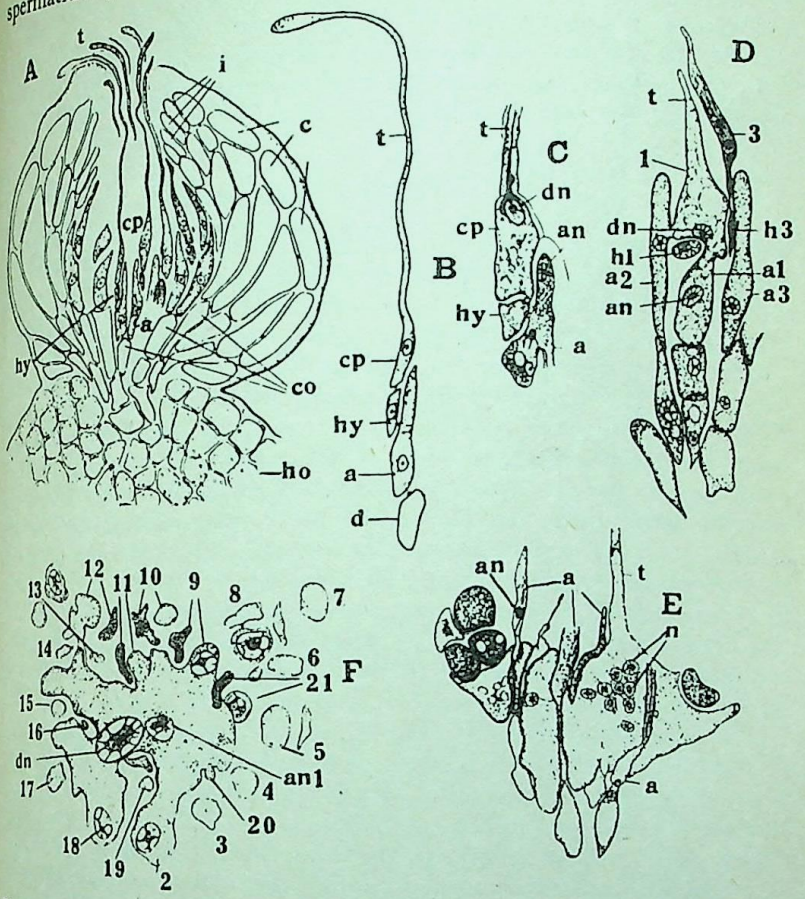

Fig. 247. *Choreonema Thureti* (Born.) Schmitz (after Minder). A, vertical section of female conceptacle with mature carpogonia; B, disc-cell and procarp; C, procarp after fertilisation; D, fusion of carpogonium (*1*) with auxiliary cells (*a1*, *a2*, *a3*); E, later stage of fusion; F, fusion-cell from above, with remains of procarps (*1–21*). *a*, auxiliary cell; *an*, auxiliary cell nucleus; *c*, cells forming wall of conceptacle; *co*, threads giving rise to conceptacle; *cp*, carpogonium; *d*, disc-cell; *dn*, diploid nucleus; *h* and *hy*, hypogynous cell; *ho*, host; *i*, threads forming aperture of conceptacle; *n*, nuclei; *t*, trichogyne.

245, H, *s*) its lower end is often attenuated, a feature which is very pronounced in *Corallina* (cf. also (692) p. 95); according to Suneson the tail is formed by a shrunken part of the wall from which the protoplast has withdrawn. Recent observations afford little support for the view ((259) p. 182, (586) p. 234, (652) p. 53) that the antheridia of Corallinaceae are formed in rows.

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In *Epilithon* ((387) p. 39, (545) p. 59, (558) p. 235, (659) p. 60) the central threads of the young male conceptacle consist of two cells (fig. 246 D), while the peripheral ones (*f*) are longer. The mother-cells (*m*) are cut off from the two lower cells of the fertile threads, while the upper cells of the peripheral ones develop branches (*br*) which form the roof of the conceptacle. Later (fig. 246 C) the two fertile layers separate to form a cavity lined with mother-cells (*m*) and roofed by the several-layered conceptacle-wall, which develops a narrow aperture. The mature conceptacle is filled with detached antheridia.

(*d*) *The Family Choreocolaceae*

Kylin ((400) p. 225) refers this family of problematical parasites (excl. *Holmsella*) to the Cryptonemiales owing to certain resemblances to Callymeniaceae. Both in *Choreocolax* ((541) p. 56, (658) p. 591) and *Harveyella* ((558) p. 496, (656) p. 90, (658) p. 600) the female cushions include numerous procarps (fig. 248 A). The carpogonial branches (fig. 248 A, C, *cb*) arise singly from the auxiliary cell (*a*) which also bears one (*Choreocolax*, fig. 248 A, *s*) or two (*Harveyella*, fig. 248 C, *s*) sterile branches. Sturch produces some evidence (fig. 248 A, middle) that the auxiliary cell proper (*a*) is cut off from the supporting cell (*su*) at the time of fertilisation. In *Harveyella* the carpogonium fuses with the auxiliary cell (fig. 248 E, *a*) and this with the cells of the sterile threads (*s*) to form an irregular fusion-cell, from which the gonimoblast-initial (*gi*) is produced. Similar changes occur in *Choreocolax*, although here the carpogonium communicates with the auxiliary cell by means of a short connecting thread. In both genera the auxiliary cells form secondary pit-connections with the adjacent cells.

The gonimoblast of *Harveyella* (cf. also (657) p. 36) is a richly branched thread (fig. 248 D, *g*), which spreads horizontally among the cells of the cushion (cf. *Dermonema*, etc., p. 610) and produces tufts of erect branches, bearing terminal carposporangia (*ca*). The auxiliary cell of *Choreocolax* cuts off several gonimoblast-initials which produce short filaments with terminal carposporangia; the mature cushions are lobed, each lobe harbouring a group of carpospores. In *Harveyella* the entire cushion constitutes a single fruit.

The antheridia ((87), (656) p. 90, (657) p. 37, (658) p. 598) cover the whole surface of the male cushions; in *Harveyella* (fig. 248 B, *an*) they are cut off from narrow mother-cells (*m*) produced by the peripheral cells.

There are evident analogies to Callymeniaceae in the structure of the female reproductive system. At the same time, as pointed out by Sturch, the procarp of *Harveyella* resembles that of Ceramiales, especially if the auxiliary cell be formed after fertilisation. The other events succeeding fertilisation and the ripe gonimoblasts are, however, altogether different from what is found in the latter order. The two genera require further investigation.

Holmsella (*Harveyella pachyderma* (657) p. 31) appears to have other affinities. The auxiliary cell (fig. 249 B, *a*), stated to be cut off after

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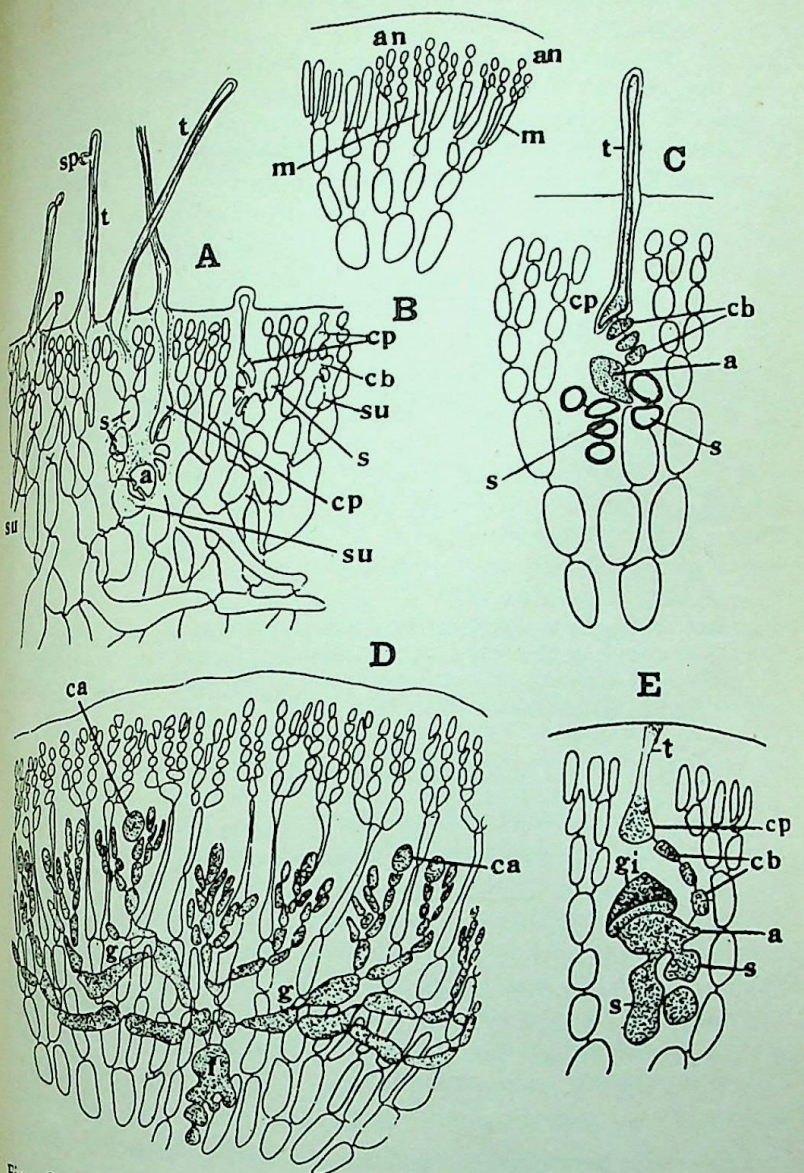

Fig. 248. A, *Choreocolax Polysiphoniae* Reinsch, section of female cushion showing procarps in various stages of development. B–E, *Harveyella mirabilis* (Reinsch) Schmitz & Reinke; B, antheridial development; C, procarp; D, young gonimoblast; E, fusion of auxiliary and sterile cells, development of gonimoblast-initial. *a*, auxiliary cell; *an*, antheridium; *ca*, carposporangium; *cb*, carpogonial branch; *cp*, carpogonium; *f*, fusion-cell; *g*, gonimoblast; *gi*, gonimoblast-initial; *m*, antheridial mother-cell; *p*, young procarp; *s*, sterile cell; *sp*, spermatium; *su*, supporting cell; *t*, trichogyne. (After Sturch.)

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fertilisation, arises from one of the lower cells (*b*) of a peripheral cell-row near the usually two-celled carpogonial branch (fig. 249 A); the short connecting filament (fig. 249 B, *co*) is sometimes two-celled. During the development of the gonimoblast, extensive fusions take place between its filaments and the adjacent cells (fig. 249 C), and this is followed by the formation of vertical rows of carposporangia (*ca*). The antheridia are formed much as in *Harveyella*. This genus presents certain analogies with Cruoriaceae.

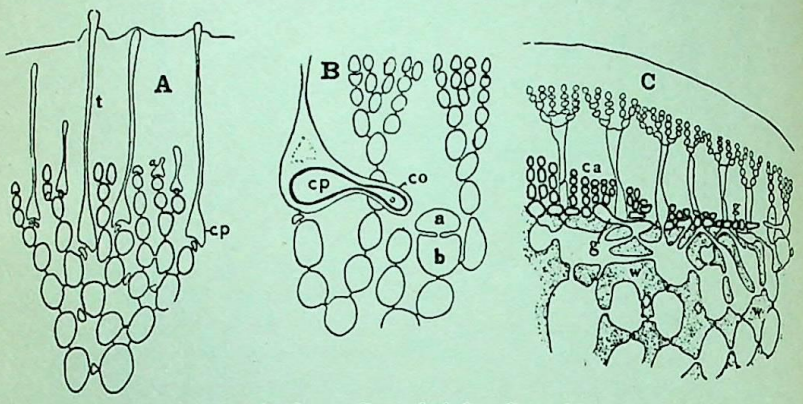

Fig. 249. *Holmsella pachyderma* Sturch (after Sturch). A, procarps; B, formation of connecting filament (*co*); C, part of a cystocarp. *a*, auxiliary cell; *b*, mother-cell of same; *ca*, carposporangia; *cp*, carpogonium; *g*, gonimoblast; *t*, trichogyne; *w*, gelatinous walls of cells.

(*e*) *The Tetrasporangiate Phase*

In many Cryptonemiales the tetrasporangia ((39) p. 8, (558) p. 282) are borne on the vegetative laterals and lie embedded in the surface-tissues (fig. 225 F). Some of the nemathecial forms also produce their sporangia in nemathecia (*Peyssonnelia*, *Constantinea*), although this is not so in *Polyides* and *Rhizophyllis*. The spores are for the most part arranged cruciately (fig. 250 H), though zonate in *Dudresnaya*, *Constantinea*, *Cruoria* (fig. 250 I) and Corallinaceae (fig. 250 C, E–G). In the production of the tetraspores four nuclei are usually formed before separating walls arise (fig. 250 E; (35) p. 374, (558) p. 213, (757) p. 92).

Transitions between the cruciate and zonate types have been recorded in *Dumontia* ((182) p. 279), *Gloeopeltis* ((634) p. 11), and *Cryptosiphonia* ((634) p. 6), while according to Kuckuck ((356) p. 984) the arrangement of the spores in *Harveyella mirabilis* is either cruciate or tetrahedral. In *Cruoria* (cf. also (358) p. 392) and *Dumontia* ((380) p. 14, (558) p. 156) the sporangia occupy the same position as the carpogonial branches (cf. fig. 250 I), whereas in *Petrocelis* ((558) p. 176) they are intercalary in the erect threads. Those of *Polyides* ((692) p. 76) arise near the inner limit of the outer cortex. In the nemathecia of *Peyssonnelia* ((387) p. 36, (558) p. 194) the sporangia are embedded among the sterile threads (fig. 250

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H, *t*); the formation of a nemathecium terminates the growth of the part of the thallus involved and in the next season it becomes overgrown by the adjacent parts. Sporangial nemathecia are also formed in *Endocladia* ((387) p. 45), the sporangia being borne laterally on the lowest cell of certain of the component threads.

Most Corallinaceae produce their tetrasporangia in conceptacles (figs. 162 A, *te*; 250 C, G), similar to those harbouring the sex organs. The cells of the disc usually divide into a stalk-cell and the sporangial rudiment. As a general rule the sporangia are uniformly distributed over the floor of the conceptacle (fig. 250 C), but in *Lithophyllum* (fig. 250 G) they are commonly restricted to the periphery, while the raised central portion is occupied by a tuft of sterile threads (*sf*; (482) p. 361, (526) p. 258, (659) p. 26). The greater specialisation of the latter genus is evident also in the structure of the procarp (p. 646; cf. however (415) p. 188).

In *Epilithon* ((387) p. 40, (558) p. 234, (577) p. 152, (659) p. 61), *Lithothamnion* ((482) p. 344, (526) p. 255, (652) p. 51, (659) p. 68) and *Phymatolithon* ((214) p. 4, (215) p. 9; incl. *Eleutherospora* (297) p. 68) there are no conceptacles, the sporangia forming sori which are embedded within the crusts (fig. 250 E, F).[1] The sorus of *Epilithon* (fig. 250 D) is formed by the outgrowth from the basal stratum (*b*) of a group of fertile (*t*) and sterile (*s*) threads, the terminal cells of the former giving rise to the sporangia (*t*). As they develop, the second lowest cell of each sterile thread undergoes great elongation (fig. 250 E, *s*), thus elevating the cells above which form a compact roof (*r*) to the sorus. The membrane of the young sporangium develops a pronounced apical thickening (fig. 250 D, *a*) which penetrates among the cells of the roof and ultimately dissolves, leaving an open channel (fig. 250 E, *po*) above each sporangium. Similar sori are found in *Lithothamnion* (fig. 250 F) and *Phymatolithon*; in the latter the roof of the sorus is concave. In *Lithothamnion* the sori (fig. 180 D) usually become overgrown by the surrounding parts, and this may ensue so quickly that the tetraspores remain imprisoned within the crusts (cf. also (35) p. 371). Old sori either appear as cavities within the strata or become filled with tissue.

More extensive, and not such sharply circumscribed, sori occur in the fossil *Archaeolithothamnion* (Upper Cretaceous and Lower Tertiary (566) p. 310), as well as in the recent genus *Sporolithon* ((294) pp. 66, 415, (295)),[2] which is stated to have cruciate tetrasporangia. The kind of sorus found in *Archaeolithothamnion* may well be primitive and have led to the more defined type seen in *Lithothamnion* and *Epilithon* which, in its turn, may have resulted in the conceptacle with

[1] Cf. also *Mesophyllum* (421).

[2] Foslie ((215) p. 9) and others include *Sporolithon* in *Archaeolithothamnion*, a point of view which could only be substantiated if the sexual reproductive organs of the latter became known (cf. (296) p. 82).

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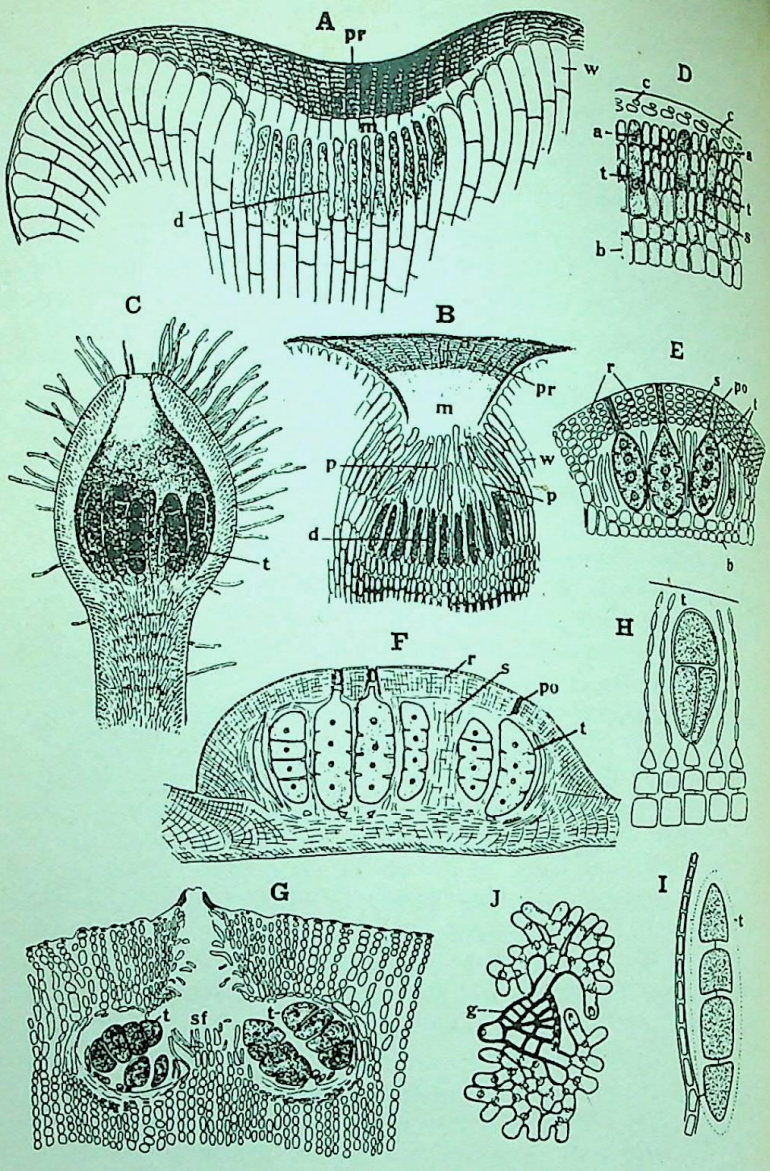

Fig. 250. Tetrasporangia of Cryptonemiales. A–C, *Corallina mediterranea* Aresch.; A, early and B, later stages in development of conceptacle, in vertical section; C, mature conceptacle. D, E, *Epilithon membranaceum* (Esper.) Heydr., vertical sections of crusts with young (D) and mature (E) sporangia. F, *Lithothamnion lichenoides* (Ellis & Soland.) Foslie, vertical section of crust with mature sporangia. G, *Lithophyllum expansum* Phil., vertical section of mature conceptacle. H, *Peyssonnelia Dubyi* Crouan. I, *Cruoria pellita* (Lyngb.) Fries. J, *Melobesia Solmsiana* Falkenb., germinating gemma (*g*). *a*, apical thickening of membrane; *b*, basal layer of thallus; *c*, cover-cells; *d*, disc-cells; *m*, mucilage; *p*, paraphyses; *po*, pore above sporangium; *pr*, prismatic layer of wall; *r*, roof of sorus; *s* and *sf*, sterile threads; *t*, tetrasporangium; *w*, wall of conceptacle. (A, B, J after Solms-Laubach; C after Thuret & Bornet; F, G after Suneson; the rest after Kylin.)

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a single aperture. Such a view is justified by certain similarities in development. Thus, in *Melobesia* ((545) p. 40, (659) pp. 13, 19) the conceptacle commonly consists of an aggregate of fertile and sterile threads, although the latter are stated ((652) p. 50) to be absent in some species. The roof of the conceptacle is formed partly from the sterile threads, and this is also so in *Amphiroa* and *Lithophyllum* ((659) pp. 27, 53). In diverse Corallinaceae, however, the sterile threads are reduced or altogether lacking and the wall of the conceptacle is formed entirely by upgrowth of peripheral tissue. According to Solms-Laubach ((652) p. 34) delicate paraphyses (fig. 250 B, *p*) occur also in the young sporangial conceptacles of *Corallina*.

The diversity of the sporangial conceptacles of Corallinaceae renders them more useful than the sexual ones in tracing affinities. From the possibly primitive *Archaeolithothamnion* we can trace three lines of development, that exemplified by *Lithothamnion* and *Epilithon*, that illustrated by *Melobesia*, *Lithophyllum* and *Choreonema*, and that including *Amphiroa* and *Corallina*. The sori of *Epilithon* and *Lithothamnion* are clearly homologous with the nemathecia of *Peyssonnelia* (cf. (387) p. 116, (455) p. 31, (586) p. 234). The affinity with the nemathecial Cryptonemiales is, however, probably rather remote ((659) p. 95).

The Corallinaceae commonly produce bispores which appear to occur more frequently in the encrusting forms, although recorded ((659) p. 53) in *Amphiroa rigida*. Bauch ((35) p. 367) distinguishes between obligate and facultative bisporic species, certain of the latter possessing distinct bisporic and tetrasporic races, in part characteristic of different habitats. According to Foslie ((216) p. 53; cf. however (415) p. 52) bisporic species occur especially in colder seas and are altogether lacking in the Tropics. The bispores are either binucleate (*Lithothamnion polymorphum*) or uninucleate (*Lithophyllum incrustans*). When the nuclei are single, they are about twice as big as a tetraspore-nucleus of the same species; this may imply that the second division is suppressed or perhaps postponed to the time of germination. Monospores are recorded ((35) p. 379) in a few members of Corallinaceae. *Melobesia Solmsiana* (p. 507; (652) p. 59) exhibits vegetative propagation by triangular plate-shaped gemmae (fig. 250 J, *g*), composed of thick-walled cells.

The marine species of *Hildenbrandia*, in which sexual reproduction is unknown, likewise form their sporangia in conceptacles (fig. 251 A) which develop much like those of Corallinaceae. According to Rosenvinge ((558) p. 204) sporangia are produced at all times of the year and arise successively, not only from the floor and the sides of the conceptacle (fig. 251 A), but even from the roof; as the production of sporangia proceeds, new ones originate from the next-adjacent layer of the thallus so that the conceptacle gradually widens. Occasional sporangia are replaced by paraphyses (*p*). The septa between the spores

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are oblique and often irregular in orientation (fig. 251 C; cf. also (53) p. 15), although parallel in *H. Crouani* (fig. 251 A; (32) p. 438, (558) p. 207).

The general aspects of the life-cycle of Cryptonemiales are considered, together with that of other diplobiontic Florideae, on p. 722.

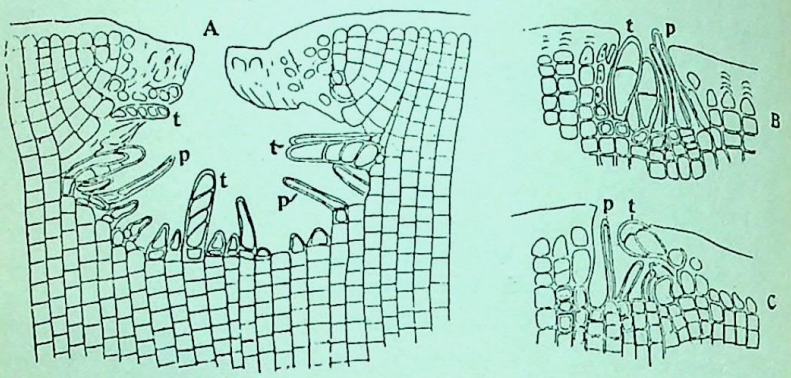

Fig. 251. Tetrasporangial conceptacles of *Hildenbrandia* in vertical section; A, *H. Crouani* J. Ag.; B, C, *H. prototypus* Nardo. *p*, paraphyses; *t*, tetrasporangia. (After Rosenvinge.)

5. The Diplobiontic Type among Gigartinales

(*a*) *The Sexual Phase*

The order Gigartinales, as defined by Kylin ((393) p. 72), includes all those Florideae in which the auxiliary cell is formed already prior to fertilisation and in which it is constituted by an intercalary cell of one of the ordinary vegetative laterals composing the thallus. In Cryptonemiales, on the other hand, the auxiliary cells are located in special accessory branches. This is rather a trivial feature upon which to base a major taxonomic subdivision, but until a clearer conception of affinities can be obtained, admitting of a different grouping, it serves a convenient purpose. Kylin ((387) p. 116) regards the Gloeosiphoniaceae and Endocladiaceae as connecting links between the two orders.

The sexual reproductive apparatus of Gigartinales shows a number of marked parallels with that of Cryptonemiales. Like the latter, they include forms in which carpogonial branches and auxiliary cells are spatially separated and others in which they are combined to form a procarp, and the discussion of the different genera is most usefully arranged on this basis. Both the auxiliary cells and the supporting cells of the carpogonial branches are nearly always located in the inner cortex.

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(i) *Gigartinales without Procarps*

In *Platoma Bairdii*[1] (363) the colourless three-celled carpogonial branches (fig. 252 D, *cb*) arise from the inner cells of the laterals (*l*), while the more numerous auxiliary cells (*a*) are located near the base of other laterals (cf. Grateloupiaceae, Dumontiaceae); exceptionally a carpogonial branch may be borne directly upon an auxiliary cell. The auxiliary cells are considerably enlarged and protruded on one side (fig. 252 C, *a*). Several connecting filaments (figs. 252 D; 224 G, *co*) arise successively from the carpogonium (*cp*) and, as in Dumontiaceae, the same filament may fuse with a number of auxiliary cells, contact being made with the protruded part of the latter. The gonimoblast-initial (fig. 252 C, D, *gi*) is cut off on the outer side of the auxiliary cell and gives rise to a mass of short threads, most of the cells of which become carposporangia (*ca*). An ill-defined pore is formed in the cortex, through which the carpospores are emitted. No antheridia have been found in *P. Bairdii* ((363) p. 192, (558) p. 162), and it is possible that the carpogonium develops parthenogenetically.

Several allied forms show essentially the same features (fig. 252 A, E). In *Schizymenia* ((124) p. 644, (389) p. 39, (553) p. 816) the pore above each mass of carpospores is well defined (fig. 252 F, *po*). In *Calosiphonia vermicularis* ((39) p. 11, (68) p. 38,[2] (389) p. 37) the carpogonium (fig. 252 G, H) fuses with the supporting cell (*su*) prior to the formation of connecting filaments, and the auxiliary cells become conspicuous only after fusion with one of the former. The closely related *Bertholdia neapolitana* (*Calosiphonia neapolitana* (39) p. 12, (587) p. 454), as well as *Nemastoma* ((393) p. 7), are distinguished by the fact that the gonimoblasts arise from the connecting filaments near the auxiliary cells. In *Sebdenia* ((39) pp. 11, 13, (634) p. 23) the fruiting parts are prominently swollen owing to extensive division of the cortical cells above the gonimoblast; the cells in question acquire rich contents and the inner ones are believed to supply nourishment to the developing gonimoblast. In all these Gigartinales the gonimoblast-initial is cut off externally (fig. 252 B, D, *gi*).

The carpogonial branches of *Furcellaria fastigiata* ((380) p. 15, (558) p. 168) and *Halarachnion ligulatum* ((39) p. 11, (68) p. 45, (387) p. 62) arise near the tips of the fronds from large cells of the inner cortex (figs. 253 A; 254 A); especially in *Furcellaria* the same supporting cell (*su*) may bear more than one carpogonial branch (fig. 253 B). The auxiliary cells (figs. 253 E; 254 D, *a*) are likewise situated in the inner cortex. The male plants of *Furcellaria* (fig. 253 C; (85) p. 261, (258) p. 235, (690) p. 22) are conspicuous by their swollen, pale yellow or pink tips (*m*), upon which the surface-cells produce pairs of mother-

[1] Cf. also (68) p. 48 (*P. marginifera*, as *Nemastoma marginifera*) and (727) p. 254 (*P. Pikeana* (Dickie) v. Bosse).
[2] As *Calosiphonia finisterrae* Crouan.

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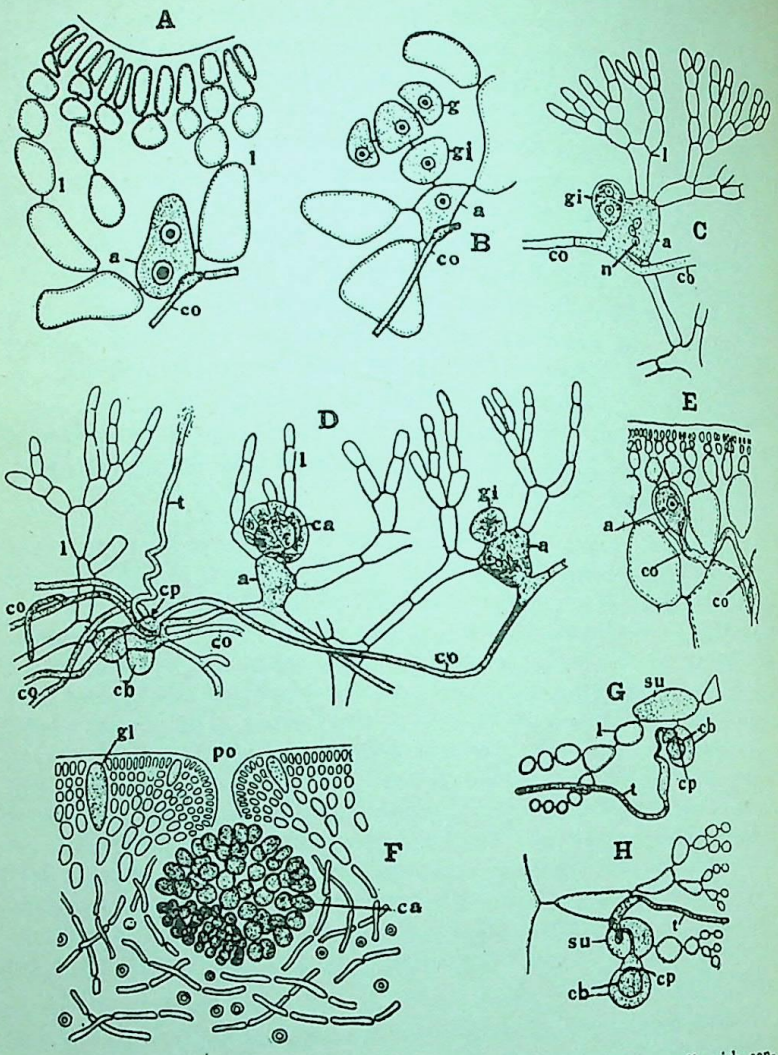

Fig. 252. A, B, F, *Schizymenia pacifica* Kyl.; A, auxiliary cell with connecting filament; B, young gonimoblast; F, section of mature fruit. C, D, *Platoma Bairdii* (Farl.) Kuck.; C, fusion of connecting filament with auxiliary cell, formation of gonimoblast-initial; D, composite figure, showing post-fertilisation development. E, *Sebdenia Monardiana* (Mont.) Berth., fusion of connecting filament with auxiliary cell. G, H, *Calosiphonia vermicularis* (J. Ag.) Schmitz, carpogonia. *a*, auxiliary cell; *ca*, carposporangia; *cb*, carpogonial branch; *co*, connecting filament; *cp*, carpogonium; *g*, gonimoblast; *gi*, gonimoblast-initial; *gl*, glandular cell; *l*, lateral; *n*, nuclei; *po*, aperture of fruit; *su*, supporting cell; *t*, trichogyne. (C, D after Kuckuck; E after Sjöstedt; the rest after Kylin.)

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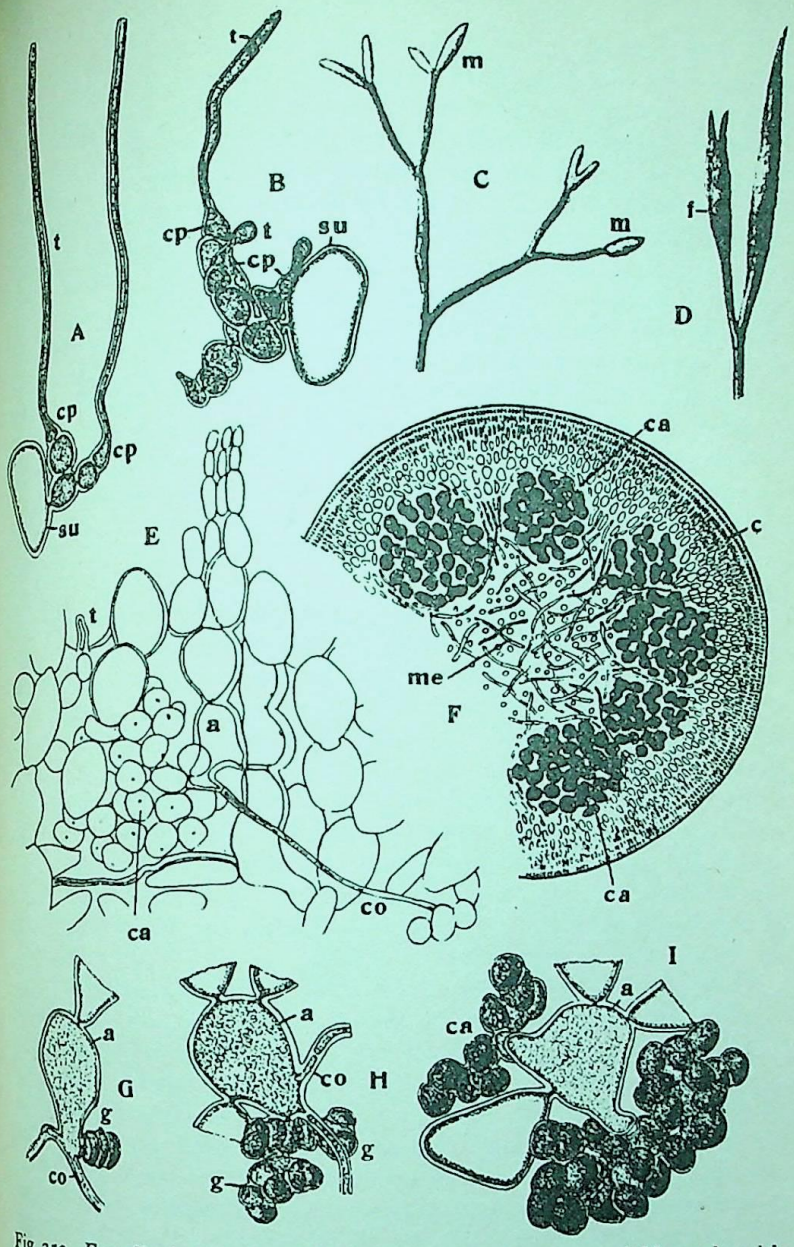

Fig. 253. *Furcellaria fastigiata* (Huds.) Lamour. A, carpogonial branch, with two carpogonia; B, the same, with three carpogonia; C, branch of a plant with tips occupied by antheridial sori (*m*); D, ditto with ripe cystocarps (*f*); E, connecting filaments and auxiliary cell, with carposporangia; F, transverse section through fruiting tip, with groups of carposporangia; G, young and H, older gonimoblasts; I, mature gonimoblasts. *a*, auxiliary cell; *c*, cortex; *ca*, carposporangia; *co*, connecting filament; *cp*, carpogonium; *g*, gonimoblast; *m*, antheridial sori; *me*, medulla; *su*, supporting cell; *t*, trichogyne. (C–E after Rosenvinge; the rest after Kylin.)

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cells (fig. 222 K, L, *m*), each forming two primary antheridia (*a*) followed by secondary ones (*sa*). *Halarachnion* is monoecious, the minute male sori being scattered over the thallus ((87) p. 299).

The connecting filament (figs. 253 E, G, H; 254 B, D, *co*) establishes contact with the inner surface of the auxiliary cell (*a*) which, in *Halarachnion* (fig. 254 C, E), develops a thin-walled process (*p*) with which the connecting filament fuses. The gonimoblast-initial (figs. 253 G, *g*; 254 D, *gi*) is in both genera cut off internally, immediately adjacent to the point of fusion. All the cells of the gonimoblast become fertile (fig. 253 E, I), the masses of carpospores (*ca*) lying in or at the periphery of the medulla (fig. 253 F); the carpospores are extruded through narrow pores formed in the cortex. The fruiting tips of *Furcellaria* (fig. 253 D), observable in autumn and winter, are usually somewhat inflated. In *Halarachnion* the cells of the carpogonial branch become swollen and multinucleate in later stages (fig. 254 A), while the fertilised carpogonium divides transversely (fig. 254 B, *cp*), each cell giving rise to a number of connecting filaments (*co*).

A considerable number of the Gigartinales without procarps differentiate special *nutritive systems* in connection with gonimoblast-development. In *Turnerella* (213) and *Opuntiella* ((394), (400) p. 231), as well as in *Catenella Opuntia* ((281) p. 73, (387) p. 66), the inner cells of the gonimoblast-threads fuse with the auxiliary cell to form a branched fusion-cell (fig. 255 C, D, *f*),[1] bearing rows of carposporangia (*ca*); in *Opuntiella*, moreover, the lateral harbouring the auxiliary cell produces numerous small-celled branchlets rich in nutriment which is absorbed during the development of the spores. In these genera (cf. fig. 254 K), however, as in the Gigartinales previously considered, nourishment reaches the gonimoblast only by way of the auxiliary cell.

More specialised features are found in Solieriaceae, among which *Agardhiella tenera* ((50) p. 363, (387) p. 69, (505) p. 411) furnishes a typical instance. Here nearly all the cells of the laterals, containing the uninucleate auxiliary cells (fig. 254 H, *a*), possess dense cytoplasmic contents and several nuclei (primary nutritive tissue, *n*). As the gonimoblast develops, the surrounding cells give rise to an enveloping small-celled secondary nutritive tissue (*nu* in fig. 255 A; cf. *Callymenia* and *Gigartina*, p. 672). The gonimoblast-initial divides into a group of sterile cells (fig. 255 A, *c*) and, during this, the contents of the primary nutritive tissue are exhausted; from the central group arise radiating gonimoblast-threads (*g*), which penetrate the secondary nutritive tissue (*nu*) and enter into secondary pit-connections with its cells. The sterile cells of the gonimoblast lose most of their con-

[1] Such a cell is formed in all Rhabdoniaceae, to which *Catenella* belongs, but in *Rhabdonia* (fig. 298 D) and others it becomes directly connected with the cells of the axial thread ((387) p. 33).

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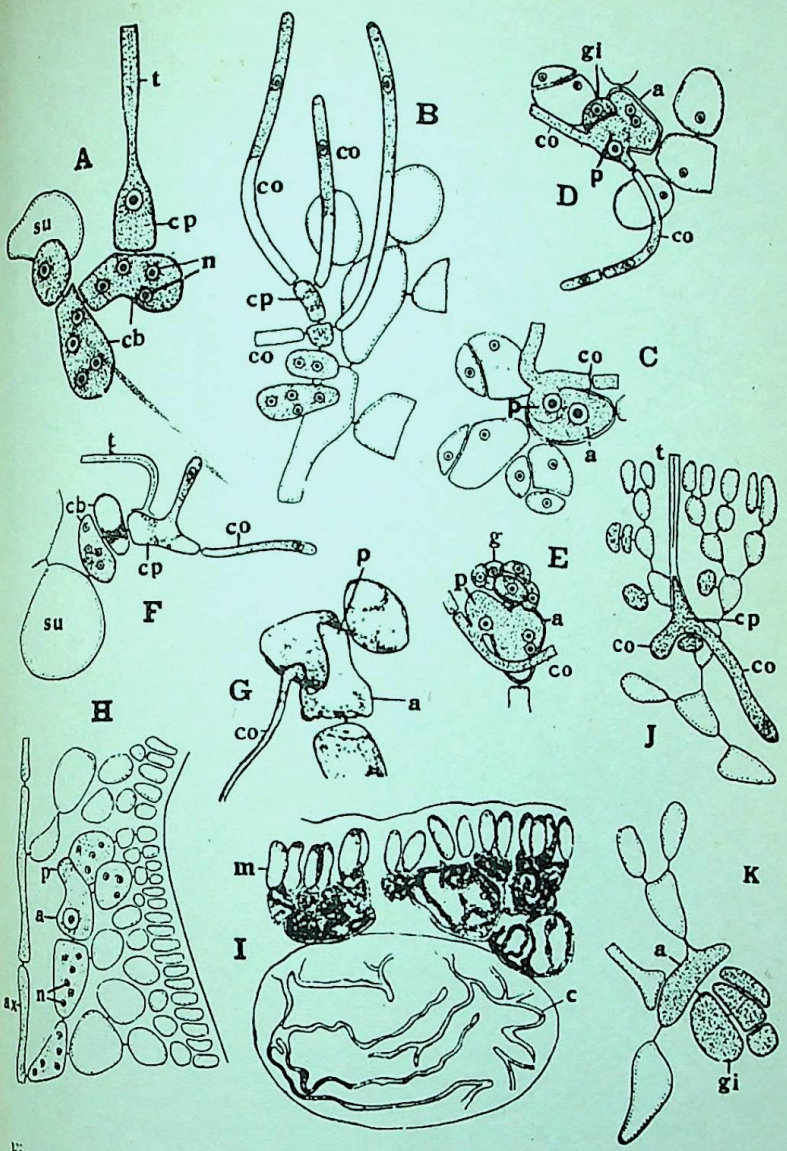

Fig. 254. A–E, *Halarachnion ligulatum* Kütz.; A, carpogonial branch; B, development of connecting filaments; C, fusion between connecting filament and auxiliary cell; D, formation of gonimoblast-initial; E, young gonimoblast. F–I, *Agardhiella tenera* (J. Ag.) Schmitz; F, development of connecting filaments; G, fusion between connecting filament and auxiliary cell; H, longitudinal section showing position of auxiliary cell; I, antheridia development. J, K, *Catenella Opuntia* (G. & W.) Grev.; J, development of connecting filament; K, development of gonimoblast. *a*, auxiliary cell; *ax* axial cell; *c*, chromatophores; *cb*, carpogonial branch; *co*, connecting filament *cp*, carpogonium; *g*, gonimoblast; *gi*, gonimoblast-initial; *m*, antheridia mother-cells; *n*, nuclei; *p*, process of auxiliary cell; *su*, supporting cell *t*, trichogyne. (G, I after Osterhout; the rest after Kylin.)

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tents, as the terminal carposporangia (*ca*) develop. In the South European *Solieria chordalis* ((69) p. 187, (393) p. 18) the sterile cells of the gonimoblast fuse with the auxiliary cell to form a huge spherical fusion-cell (fig. 255 B, *f*), which is very conspicuous in the ripe fruit.

The carpogonium (fig. 254 F, *cp*) of *Agardhiella* enlarges after fertilisation and forms several connecting filaments (*co*); the few auxiliary cells (fig. 254 G, H, *a*) possess an apically directed process (*p*). The connecting filament (*co*) fuses with the lower end of the auxiliary

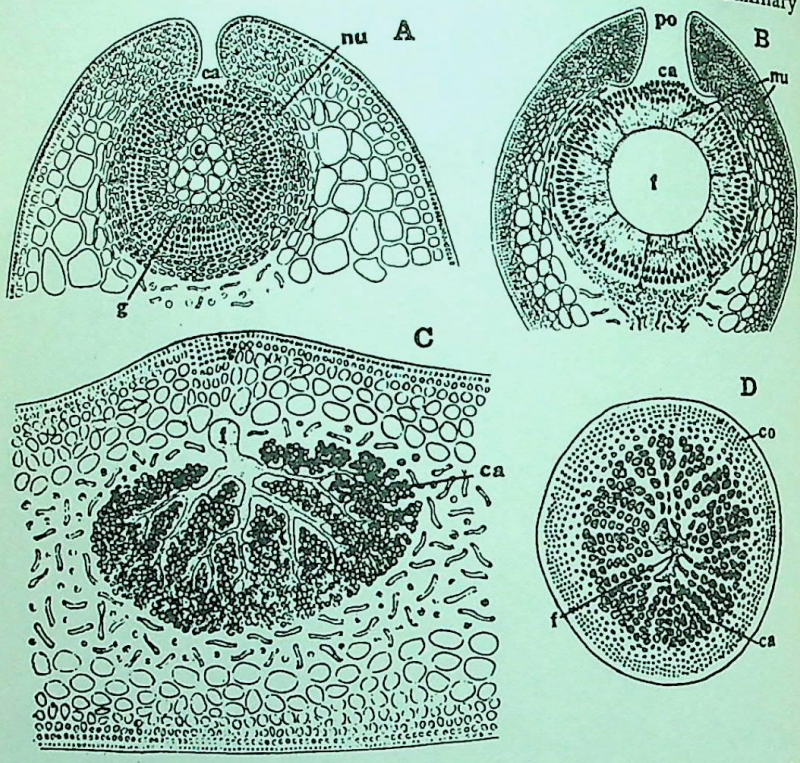

Fig. 255. Fruits of diverse Gigartinales in section (after Kylin). A, *Agardhiella tenera* (J. Ag.) Schmitz. B, *Solieria chordalis* (Ag.) J. Ag. C, *Opuntiella californica* (Farl.) Kyl. D, *Catenella Opuntia* (G. & W.) Grev. *c*, sterile cells of gonimoblast; *ca*, carposporangia; *co*, cortex; *f*, fusion-cell; *g*, gonimoblast; *nu*, nutritive tissue; *po*, aperture of cystocarp.

cell (fig. 254 G), but the gonimoblast-initial is cut off from the tip of the latter. The carpogonial branches (fig. 254 J) and auxiliary cells of *Catenella* occur within special small segments of the fronds; as in all Rhabdoniaceae, the auxiliary cells are not distinguishable before fertilisation and develop rich contents only after fusion with a connecting filament. The gonimoblast-initials are cut off internally (fig. 254 K, *gi*) and the radiating gonimoblast-threads (fig. 255 D) branch abundantly amid the medullary cells of the fertile frond. The swollen fruits of *Agardhiella* open by a definite pore (fig. 255 A) and the fertile

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tract is surrounded by several layers of flat cells, derived from the secondary nutritive tissue (*nu*). In *Catenella*, which rarely fruits (137), the entire fertile frond constitutes a single cystocarp, the wall of which is formed by the cortex (fig. 255 D, *co*).

The antheridia of *Agardhiella* ((505) p. 410) form irregular sori on the younger parts (fig. 254 I). Those of the monoecious *Catenella Opuntia* are produced on special branchlets of the frond, the rounded sori having a wrinkled surface, so that the antheridia appear in small pits ((85) p. 261, (281) p. 72, (587) p. 442).

(ii) *Gigartinales with Procarps*

In diverse Gigartinales (*Cystoclonium*, *Rhodophyllis*, *Calliblepharis*, *Hypnea*) the auxiliary cell (fig. 256 B, *a*) is the basal cell of a lateral (*l*), borne on the supporting cell (*su*) of the carpogonial branch (*cb*); moreover, in all of these the gonimoblast-initial is cut off internally (fig. 256 C, *gi*). The genera in question show progressive elaboration in the mode of nourishment of the gonimoblast. *Cystoclonium purpureum* ((380) p. 25, (599) p. 369), except for the possession of a procarp, resembles *Catenella* in its sexual reproduction. The supporting cell of the colourless carpogonial branch (fig. 256 B, *su*) bears a number of laterals (*l*), the cells of which have dense cytoplasmic contents; this is specially marked in the auxiliary cell (*a*), which lies immediately adjacent to the carpogonium (cf. also fig. 256 D) and no doubt becomes linked with it by a short connecting filament. The gonimoblast-initial (fig. 256 C, *gi*) develops into an elongate well-branched thread (fig. 256 D, *g*) which penetrates into the central tissue. By degrees its cells fuse with one another, as well as with the auxiliary cell (fig. 256 E) to form an irregularly branched, tubular fusion-cell (*f*), bearing numerous lateral tufts (*g*) of carposporangia (fig. 256 F, *ca*). There is abundant production of hyphae near the developing gonimoblast. The cortical cells above the procarp show active division (fig. 256 D) so that the mature fruits appear as prominent unilateral swellings on the thalli; they are devoid of an aperture. The antheridia ((87) p. 293, (380) p. 30) form extensive sori on the younger branches of the male plants.

Essentially similar procarps are found in *Rhodophyllis bifida* (fig. 257 A; (380) p. 32) where they occupy the margins of the fronds, in *Calliblepharis* ((387) p. 73, (518) p. 354) where they lie in the marginal pinnae, and in *Hypnea musciformis* (fig. 258 A; (389) p. 51) where they are situated in the short thallus-branches, except that in the last two the auxiliary cells acquire dense contents only after fertilisation. In *Rhodophyllis* (fig. 257 A) the supporting (*su*) and auxiliary cells (*au*) produce on their outer sides a layer of cells with dense contents (*r*) which, like other adjacent cells, divide abundantly after fertilisation to form the wall (pericarp) of the mature cystocarp (fig. 257 C, *w*); the latter appears as an almost spherical swelling (fig. 170 C, *c*) and has no aperture. The gonimoblast develops as in *Cystoclonium*, but some of its branches

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remain sterile and become connected to the pericarp ((393) p. 39), a nutritive device which is more marked in *Calliblepharis* and *Hypnea*.

Here, however, no fusion-cell is formed, although two kinds of nutritive tissues are developed (fig. 257 B). One of these (*nu1*) lies external to the procarp and is derived from the inner cells of the

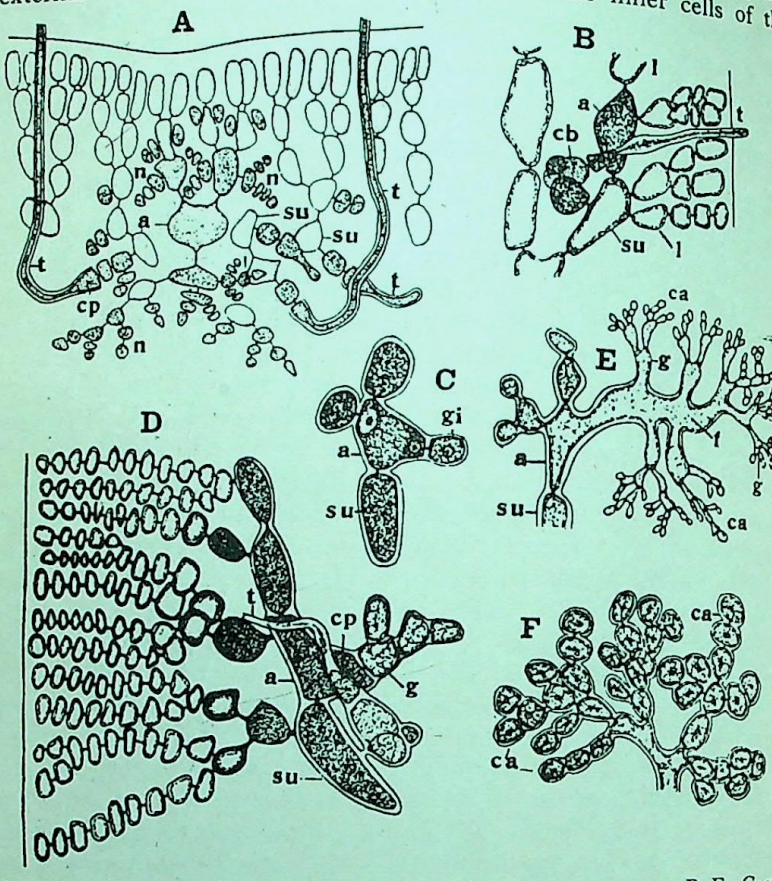

Fig. 256. A, *Rissoella verruculosa* (Bertol.) J. Ag., procarp. B–F, *Cystoclonium purpureum* (Huds.) Batt.; B, procarp; C, formation of gonimoblast-initial; D, further development of gonimoblast; E, almost mature gonimoblast; F, part of same with carposporangia. *a*, auxiliary cell; *ca*, carposporangia; *cb*, carpogonial branch; *cp*, carpogonium; *f*, fusion-cell; *g*, gonimoblast; *gi*, gonimoblast-initial; *l*, lateral; *n*, nutritive threads; *su*, supporting cell; *t*, trichogyne. (After Kylin.)

laterals borne on the auxiliary and supporting cells; the outer cells (*w*) aid in the production of the pericarp (fig. 258 B, *w*). The second nutritive tissue (fig. 257 B, *nu2*) lies internal to the procarp and consists of small cells arising from the inner vegetative cells. According to Kylin ((393) p. 41) certain species of *Rhodophyllis*, which also approach *Calliblepharis* in other respects, possess a similar internal nutritive tissue.

The gonimoblast-initial of *Calliblepharis* (fig. 257 B, *gi*) gives rise to several threads that penetrate among the internal nutritive cells, with

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which they establish secondary pit-connections (cf. *Agardhiella*); meanwhile the external nutritive system is exhausted. The carpospores are produced in unbranched threads, arising from the basal cells of the gonimoblast, and appear as a fan-shaped group on the outside of the

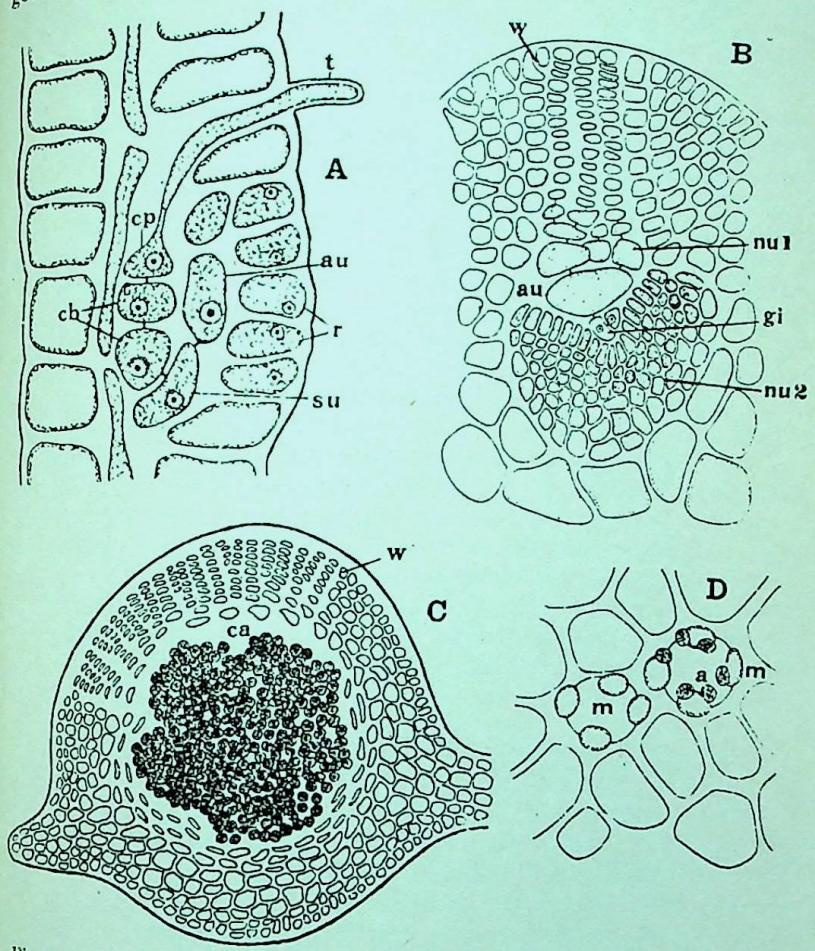

Fig. 257. A, C, D, *Rhodophyllis bifida* (G. & W.) Kütz.; A, procarp; C, vertical section of cystocarp; D, development of antheridia, from the surface. B, *Calliblepharis lanceolata* Batt., transverse section of a young cystocarp. *a*, antheridia; *au*, auxiliary cell; *ca*, carposporangia; *cb*, carpogonial branch; *cb*, carpogonium; *gi*, gonimoblast-initial; *m*, antheridial mother-cells; *nu*, nutritive tissue; *r*, roof of procarp; *su*, supporting cell; *t*, trichogyne; *w*, wall of cystocarp. (After Kylin.)

internal nutritive tissue. The large swollen cystocarps (fig. 170 A, *c*) are formed singly in the fertile pinnae.

In *Hypnea* the gonimoblast develops in a distinctive manner. The initial divides to form a compact group of small cells; some of these, after establishing connections with the internal nutritive cells, undergo

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marked elongation and lift the remainder (fig. 258 B, *g*) into the centre of the developing cystocarp-cavity. These gonimoblast-cells give rise on all sides to branched threads (*s*), which become linked by secondary pits with the cells of the pericarp (*w*). The richly branched tufts, forming terminal carposporangia (*ca*), arise not only from the central gonimoblast-group, but also from the threads linking the latter with the wall.

The large cystocarps found in these and other genera arise by extensive post-fertilisation division of the cells in the neighbourhood of the procarp; this results in a cavity of increasing width, which is occupied by the developing gonimoblast. Division is either essentially confined to the cortex, external to the fertilised procarp (e.g. *Calliblepharis*, fig. 257 B) or takes place all round it (e.g. *Hypnea*, fig. 258 B).

Antheridia appear to be unknown in *Calliblepharis*, while those of *Hypnea* have not been adequately investigated. In the monoecious *Rhodophyllis bifida* they form small scattered sori (fig. 257 D), the mother-cells (*m*) arising in fours from the surface cells and forming two or three antheridia (*a*) each ((380) p. 35).

A procarp of a more generalised type is found in *Rissoella* ((389) p. 43), a Mediterranean perennial with a fringed foliaceous thallus. Here (fig. 256 A) a single large auxiliary cell (*a*) is associated with a number of carpogonial branches, the supporting cells (*su*) of which are constituted by adjacent cortical cells; it is not clear whether they all belong to the same branch-system. The surrounding cells develop a number of small-celled laterals (*n*), homologous with carpogonial branches and constituting a nutritive tissue (cf. *Opuntiella*), although no special connection is established between it and the fusion-cell which is formed from the inner cells of the gonimoblast, the auxiliary cell, and probably also other adjacent cells.

In most other Gigartinales the supporting cell functions also as the auxiliary cell. In *Plocamium* ((380) p. 51, (389) p. 46, (518) p. 352,[1] (586) p. 238) the supporting cells (fig. 258 D, *a*) are differentiated in large numbers along the outer (more rarely the inner) margins of the fronds from the large cells surrounding the axial thread (cf. p. 492); they also bear vegetative laterals (*l*). Antheridia ((86) p. 249, (380) p. 53) are formed over the entire surface of the ultimate branches of the thallus. After fertilisation the carpogonium enlarges and the other cells of its branch degenerate, while those in the vicinity of the auxiliary cell (fig. 258 E, *nu*) acquire rich contents. The gonimoblast-initial (*gi*), which fuses with the auxiliary cell (*a*), produces a number of secondary elements (*g*) which successively give rise to densely branched tufts (*1*, *2*, *3*), most of the cells of which become carposporangia. The mature cystocarps (fig. 258 E) form sessile swellings on the edges of the thalli; the spores are liberated by disintegration of the upper part of the wall.

[1] Phillips' statement that a special auxiliary cell is cut off, is probably incorrect.

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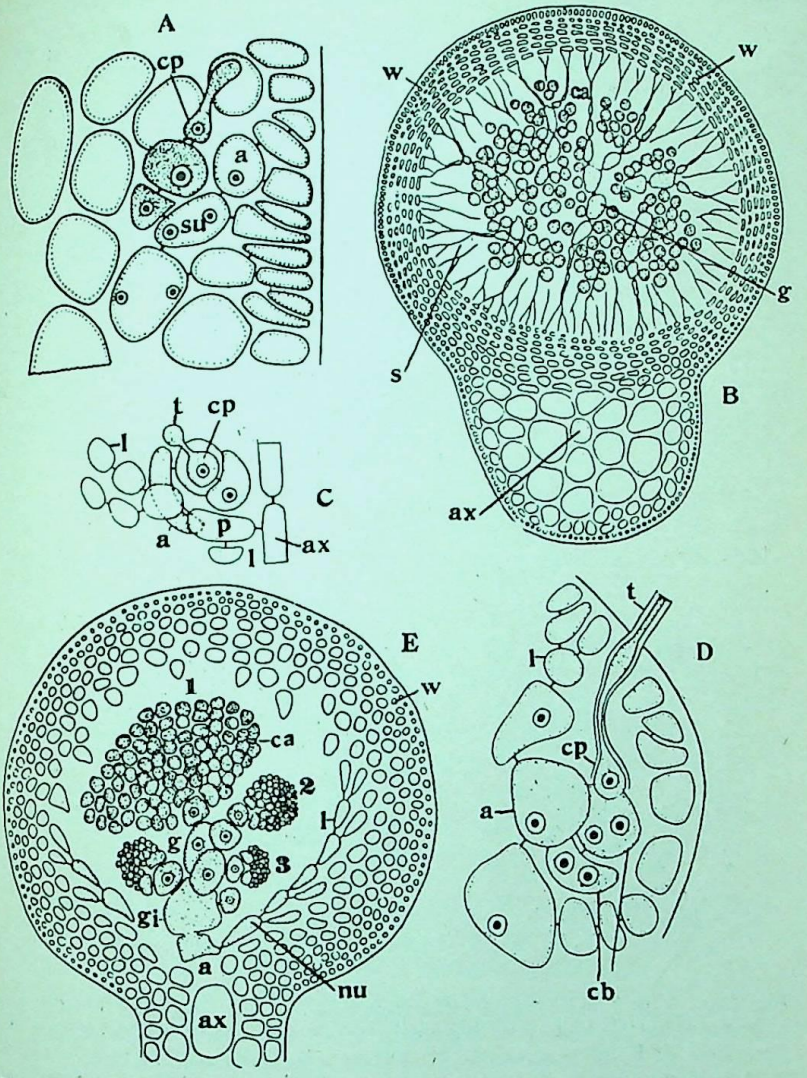

Fig. 258. A, B, *Hypnea musciformis* (Wulf.) Lamour.; A, procarp; B, transverse section of thallus with cystocarp. C, *Sphaerococcus coronopifolius* C. A. Ag., procarp. D, E, *Plocamium coccineum* (Huds.) Lyngb.; D, procarp; E, cystocarp; *1*, *2*, *3*, successive gonimolobes. *a*, auxiliary cell; *ax*, axial cell; *ca*, carposporangia; *cb*, carpogonial branch; *cp*, carpogonium; *g*, gonimoblast; *gi*, gonimoblast-initial; *l*, lateral; *nu*, nutritive threads; *s*, sterile gonimoblast-threads; *su*, supporting cell; *t*, trichogyne; *w*, wall of cystocarp. (After Kylin.)

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In *Sphaerococcus coronopifolius* ((328), (389) p. 47, (634) p. 40) and *Gracilaria* ((389) p. 55, (634) p. 51, (692) p. 81)[1] the procarps are essentially similar, although in the latter (fig. 259 C, D) the supporting cell (*su*) is

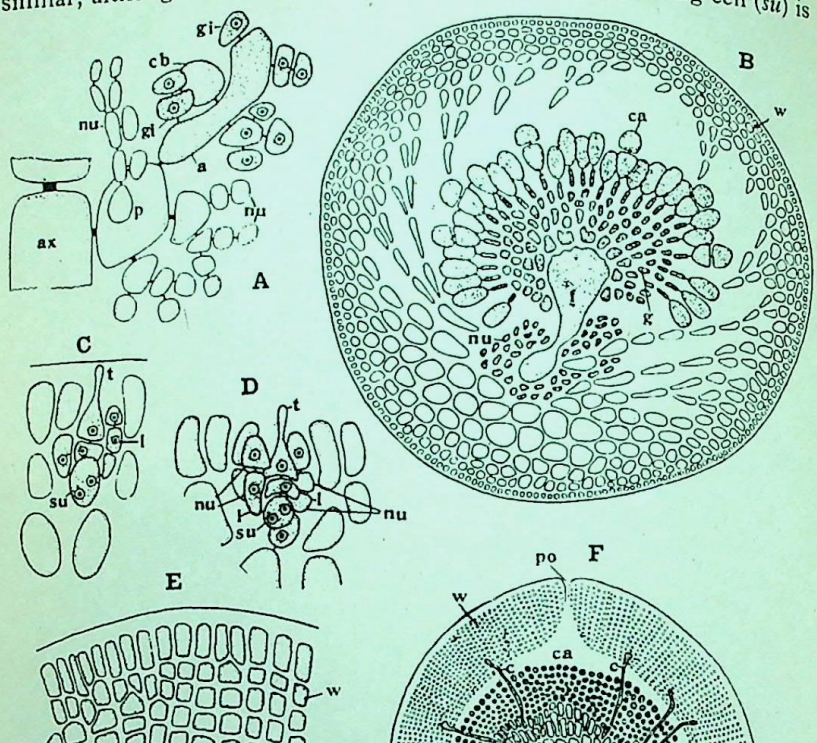

Fig. 259. A, B, *Sphaerococcus coronopifolius* C. A. Ag.; A, early development of gonimoblast; B, section of cystocarp. C, D, *Gracilaria Sjöstedtii* Kyl., two procarps. E, F, *G. confervoides* (L.) Grev.; E, formation of fusion-cell; F, section of cystocarp. *a*, auxiliary cell; *ax*, axial cell; *c*, cells of gonimoblast, connecting sterile part of same with wall of cystocarp; *ca*, carposporangia; *cb*, carpogonial branch; *f*, fusion-cell; *g*, gonimoblast; *gi*, gonimoblast-initial; *l*, lateral; *n*, nucleus; *nu*, nutritive tissue; *p*, pericentral; *po*, aperture of cystocarp; *s*, sterile part of gonimoblast; *su*, supporting cell; *t*, trichogyne; *w*, wall of cystocarp. (After Kylin.)

not specially differentiated and the laterals (*nu*) possess rich contents. Both genera exhibit more marked post-fertilisation fusions than does

[1] The account of Johnson (327) is largely erroneous, while Phillips (523) has mistaken the characteristic hairs for carpogonia (cf. (634) p. 52).

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Plocamium. In *Sphaerococcus* the auxiliary cell (fig. 259 A, *a*) produces several gonimoblast-initials (*gi*), which give rise to separate systems with terminal carposporangia (*ca* in fig. 259 B). Meanwhile the older gonimoblast-cells fuse with the auxiliary cell, and this with the adjacent pericentral and axial cells (*p* and *ax* in fig. 259 A), to form an elongate fusion-cell (fig. 259 B, *f*) bearing the radiating fertile threads. The laterals (fig. 259 A, *nu*) borne on the pericentral form a local nutritive tissue (fig. 259 B, *nu*) around the base of the fusion-cell. The mature cystocarps appear as spherical swellings in the smaller branches.

The fertilised carpogonium of *Gracilaria* fuses progressively (fig. 259 E) with the adjacent multinucleate nutritive cells (*nu*). Meanwhile the cortical cells above divide copiously to produce the cystocarp-wall (*w*); the inner cells of the rows thus formed, however, constitute a nutritive tissue around the fusion-cell (cf. *Calliblepharis*, *Hypnea*). The several gonimoblast-initials develop into a dense aggregate (fig. 259 F), the inner part of which (*s*) forms a compact pseudo-parenchyma bearing the rows of successively ripening carposporangia (*ca*). In certain species (*G. confervoides*, fig. 259 F; *G. compressa*) elongate cells (*c*) radiate from the compact region of the gonimoblast and, penetrating the pericarp, become connected with some of its cells (cf. also (523) p. 795). The swollen cystocarps appear along the sides of the thallus-branches (fig. 170 B, *c*) and, in *G. confervoides*, are sometimes stalked. The fruit-development in *Melanthalia abscissa* ((507) p. 4) exhibits essentially the same course of events; cf. also *Cordylecladia* ((389) p. 60). Perhaps *Holmsella pachyderma* (p. 650) belongs to this series.

In the Australian genera *Mychodea* ((393) p. 63) and *Acrotylus* ((277) pl. 99, (393) p. 67), which show affinity to Gigartinaceae and are possibly primitive, the supporting cell (fig. 260 A, C, *su*) bears several carpogonial branches. In *Mychodea* the principal gonimoblast-threads form a network within the cystocarp, and some are linked by secondary pit-connections to the nutritive tissue lining the inner surface of the pericarp ((400) p. 250, (590) p. 119), while in *Acrotylus* (fig. 260 D) the bunches of carpospore-bearing threads project into a cavity which is lined by a probable nutritive tissue (*nu*).

The antheridia of *Sphaerococcus* (cf. also (87) p. 293) are formed in small circular depressions behind the tips of the branches. This is also so in *Mychodea* (fig. 260 B) and in *Gracilaria confervoides* ((87) p. 294, (411) p. 134, (692) p. 81); in the latter the male plants are of small stature. In other species of *Gracilaria* the antheridia form small superficial sori.

(iii) *Phyllophoraceae and Gigartinaceae*

In these families the procarps (figs. 261 A, D; 262 B; 295 C) invariably consist of an, often large, supporting (auxiliary) cell (*su*) bearing a three-celled carpogonial branch (*cp*); in addition the former may produce a vegetative lateral (*l*), which is lacking in *Chondrus* (fig. 261 A) and in *Gigartina* is occasionally replaced by a second carpogonial branch ((634) p. 47). No conspicuous fusion-cell is formed after fertilisation, but the threads of the gonimoblast

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(fig. 261 B, *g*) penetrate into the medullary region (*me*), the elements of which form a nutritive tissue.

Chondrus produces its procarps within the ordinary fronds, but in *Phyllophora* (fig. 295 A, B, *n*), *Stenogramma*, and *Gigartina* they are situated in special outgrowths (nemathecia). These arise from the stalks in *Phyllophora membranifolia* (fig. 174 C, *f*) and from near the margins of the fronds in *P. epiphylla*, while the teat-like, simple or

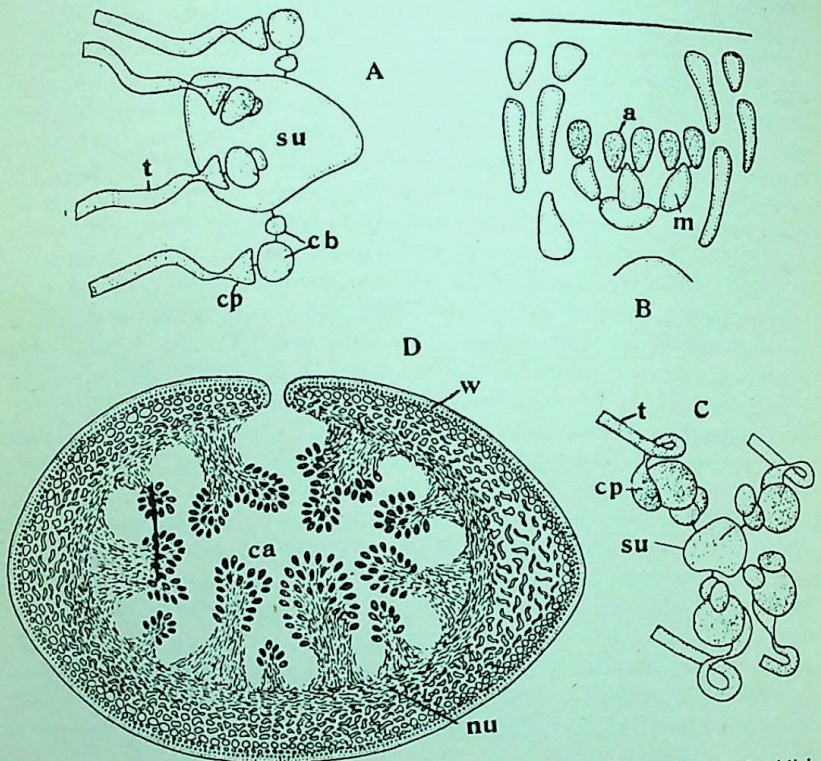

Fig. 260. A, B, *Mychodea terminalis* Harv.; A, procarp; B, antheridial development. C, D, *Acrotylus australis* J. Ag.; C, procarp; D, section of cystocarp. *a*, antheridium; *ca*, carposporangia; *cb*, carpogonial branch; *cp*, carpogonium; *m*, antheridial mother-cell; *nu*, nutritive tissue; *su*, supporting cell; *t*, trichogyne; *w*, wall of cystocarp. (After Kylin.)

branched, nemathecia of *Gigartina* (fig. 174 I, *t*) occupy either the margin (*G. Teedii*) or the surface of the thallus. Those of *Stenogramma* are linear (fig. 170 D, *n*) and form apparent veins on both surfaces of the fertile fronds; since they terminate a short distance below the apex, they are not connected in successive branches. In *Phyllophora* and *Gigartina* each nemathecium produces a single cystocarp, while in *Stenogramma interrupta*, where procarps occur along the whole length of the nemathecium, their occasional absence or failure to be fertilised leads to gaps in the dark red zones of maturing carpospores

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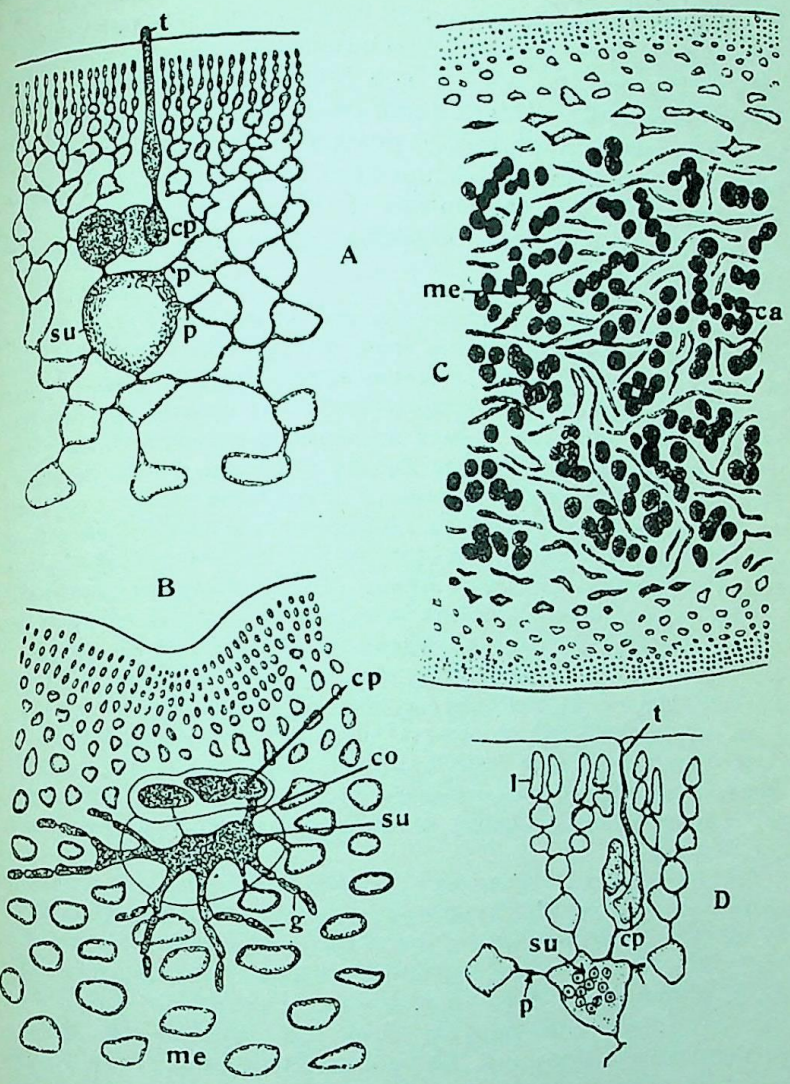

Fig. 261. A–C, *Chondrus crispus* (L.) Stackh.; A, vertical section of thallus with procarp; B, ditto, fusion of carpogonium with auxiliary cell (*su*); C, transverse section of thallus, with mature carposporangia. D, *Gigartina Teedii* Lamour., procarp. *ca*, carposporangia; *co*, connecting filament; *cp*, carpogonium; *g*, gonimoblast; *l*, lateral; *me*, medulla; *p*, pit-connection; *su*, supporting (auxiliary) cell; *t*, trichogyne. (D after Sjöstedt; the rest after Kylin.)

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to which the specific name refers. In *Gigartina* there is a definite pore to the cystocarp.

In *Chondrus crispus* ((380) p. 20, (586) p. 238) the supporting (auxiliary) cell[1] (fig. 261 A, *su*) belongs to the inner cortex and is linked to the surrounding vegetative cells by secondary pit-connections (*p*). The adjoining carpogonium (*cp*) communicates with the auxiliary cell after fertilisation (fig. 261 B) by a broad connection (*co*), through which the diploid nucleus no doubt passes into the auxiliary cell. The elongate gonimoblast-threads (*g*) penetrate into the inner tissues (*me*)[2] and give rise to numerous groups of carposporangia (fig. 261 C, *ca*), interspersed between the remains of the medulla (*me*). The carpospores are liberated from the swollen fruits after the decay of the fronds.

The structure of the procarps (fig. 261 D) and the formation of the gonimoblast are essentially the same in *Gigartina* ((586) p. 238, (634) p. 46; cf. also (387) p. 51). In certain species (e.g. *G. Teedii*) a special nutritive tissue arises from hyphae, produced in large numbers from the medullary cells, and in later stages the gonimoblast-threads communicate with its cells; in the mature cystocarp this tissue forms a fibrous envelope around the groups of carpospores (cf. also (324) p. 604). Not all species of *Gigartina* (e.g. *G. stellata*) possess a definite pericarp ((625) p. 134) and nutritive tissue may be lacking ((558) p. 511). A similar fruit-development is found in *Iridaea* and *Rhodoglossum* ((387) p. 48).

The procarps of *Stenogramma interrupta* ((330) p. 362, (387) p. 52) are distinguished by the usual multinucleate character of the component cells (fig. 262 B). Their further development is similar to that of *Chondrus* (fig. 262 A), but both here and in *Phyllophora* ((158) p. 39, (387) p. 54, (558) pp. 517, 537, (563) p. 11)[3] the gonimoblast-threads enter into communication with the loose medullary tissue (*me*) of the nemathecia. The numerous groups of carpospores produced from the tufted laterals of the gonimoblasts ultimately almost completely displace the medulla (fig. 262 C).

All these genera are dioecious. The pale antheridial sori of *Chondrus crispus* ((89), (258) p. 185) usually appear just behind the apices of the fronds; Darbishire ((161) p. 26) found them on minute white segments which later developed into vegetative branches. The mother-cells (fig. 222 J, *m*), formed by longitudinal division of the surface-cells, produce pairs of elongate antheridia (*a*) which just penetrate the gelatinous cuticle overlying the sorus. Secondary antheridia are frequent. The antheridia of *Gigartina* are borne on small leafy branches ((89) p. 184).

Those of *Phyllophora* ((86) p. 248, (87) p. 292, (158) p. 38, (172) p. 278, (558) p. 536) are produced on minute white or yellowish nemathecia,

[1] Darbishire's statement ((161) p. 28) that the auxiliary cell is cut off from the supporting cell is no doubt erroneous.

[2] Schmitz ((590) p. 118) himself corrected his earlier statement ((586) p. 242) that the gonimoblast-threads unite with the medullary cells.

For *P. Brodiaei* and *Gymnogongrus*, which differ in important respects, see p. 731.

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borne on the margins of the fronds. The surface-cells give rise to numerous tufts, some of which grow longer than others so that small antheridial cavities are formed (fig. 262 D). The male sori of

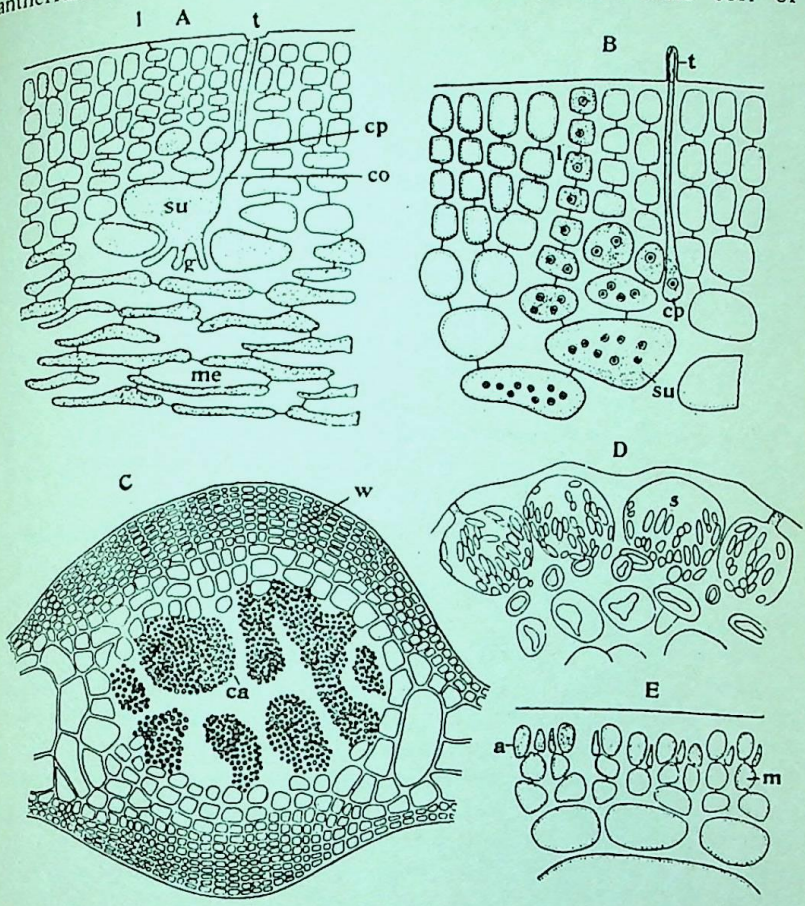

Fig. 262. A–C, E, *Stenogramma interrupta* (C. Ag.) Mont.; A, fusion between carpogonium and auxiliary cell (*su*); B, procarp; C, section of thallus, with groups of carposporangia; E, antheridial development. D, *Phyllophora membranifolia* (G. & W.) J. Ag., antheridial development. *a*, antheridium; *ca*, carposporangia; *co*, connecting filament; *cp*, carpogonium; *g*, gonimoblast; *l*, lateral; *m*, antheridial mother-cells; *me*, medulla; *s*, spermatium; *su*, supporting cell; *t*, trichogyne; *w*, wall of cystocarp. (D after Rosenvinge; the rest after Kylin.

Stenogramma ((330) p. 362) form irregular patches on both surfaces of the upper thallus-segments (fig. 262 E).

(*b*) *The Tetrasporangiate Phase*

The tetrasporangia of Gigartinales are either cruciate (fig. 263 J) or zonate (fig. 263 C, H), the latter type being found in all the genera

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discussed above except *Platoma*, *Calosiphonia*, *Nemastoma*, *Sebdenia*, *Gracilaria*, *Melanthalia*, *Cordylecladia*, Phyllophoraceae and Gigartinaceae. The zonate sporangia of *Furcellaria* ((380) p. 17) and *Plocamium* ((558) p. 600) are stated to divide first into two cells.

The sporangia are often terminal on the laterals (figs. 225 B; 263 C, *t*) and embedded at the surface of the thallus ((363) p. 191, (330) pp. 30, 35, (387) pp. 67, 75, (389) p. 54, (505) p. 419). Those of *Furcellaria* ((558) p. 167) are borne laterally (fig. 263 B, *t*) on the inner cortical cells and are rather deeply immersed within the inflated tips (fig. 263 A). In *Plocamium* (fig. 263 D) the sporangia (*t*) are formed within special branches (*stichidia*, *f*) of simple structure, which occupy the margins of the ultimate fronds ((475) p. 230). The large sporangia (fig. 263 E, *t*), which develop from the hypodermal cells and form a zigzag line along the axis of the stichidium (fig. 263 F), are covered by but a single layer of cells (*c*).

Special nemathecia harbour the sporangia in *Phyllophora* and *Stenogramma*. In *P. membranifolia* ((158) p. 35) they appear as deep-red swellings on the fronds (fig. 263 G, *n*), while those of *P. epiphylla*[1] ((158) p. 28, (558) p. 538) encircle the short stalks of special peltate branches. The numerous threads of the nemathecia consist of long chains of cruciate tetrasporangia, only the outermost cells being sterile (cf. fig. 295 F). The scattered wart-like nemathecia of *Stenogramma* ((272) p. 163, (310), (330), (735) p. 157) show a similar structure.

The sporangia of *Chondrus* ((380) p. 22, (558) p. 503) develop in the younger fronds, during the early months of the year, from the cells of small tufted laterals (fig. 263 I, *t*) borne on the medullary elements; the regions in question form dark red swellings on the thalli. In *Gigartina* the laterals producing the sporangia arise from the inner cortical cells and are located either in special papillate or leafy outgrowths (*G. californica*) or within the ordinary thallus ((387) p. 51, (404) p. 25, (502) p. 347). The tetraspores in all Gigartinaceae are set free by decay.[2]

6. The Diplobiontic Type among Rhodymeniales

(*a*) *The Sexual Phase*

Despite the considerable diversity in habit, there is great uniformity in the structure of the procarp and in the post-fertilisation stages among Rhodymeniales. The multinucleate supporting cell of the procarp (*su* in fig. 264 A, B) is constituted by a young cortical cell which rapidly enlarges and acquires richer contents. After producing either one (fig. 264 A, B) or two (fig. 266 A, C) auxiliary mother-cells (*am*), it gives rise to a three- or four-celled (figs. 266 C; 267 A) carpogonial

[1] Described by Schmitz ((591) p. 399) as a parasite (*Colacolepis incrustans*).

[2] The life-cycle of Gigartinales is considered in conjunction with that of other diplobiontic Florideae on p. 722.

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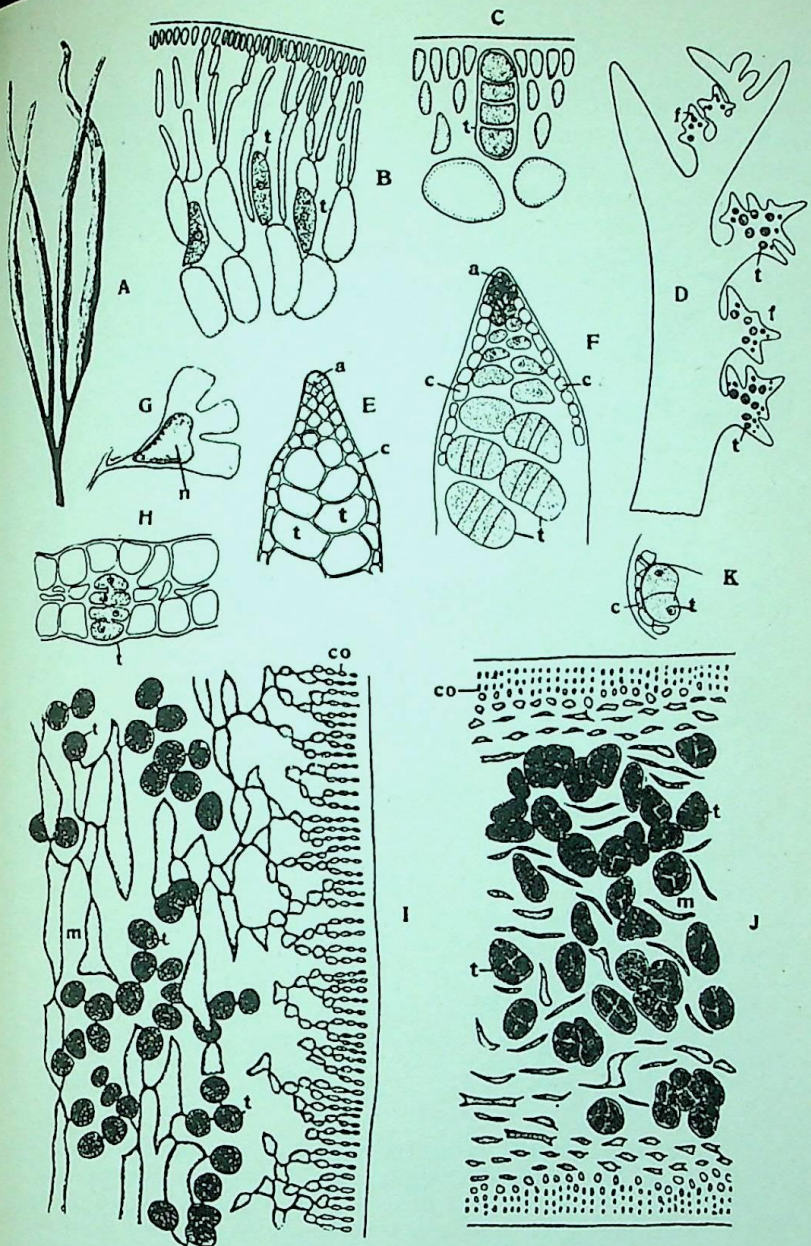

Fig. 263. Tetrasporangia of Gigartinales. A, B, *Furcellaria fastigiata* (Huds.) Lamour.; A, branch with fertile tips; B, transverse section of same, with young sporangia. C, *Mychodea foliosa* (Harv.) J. Ag. D–F, K, *Plocamium coccineum* (Huds.) Lyngb.; D, part of thallus with stichidia (*f*); E, F, vertical sections of branches of stichidium, stages in development of sporangia; K, small part of same in transverse section. G, *Phyllophora membranifolia* (G. & W.) J. Ag., with nemathecium (*n*). H, *Rhodophyllis bifida* (G. & W.) Kütz., transverse section of thallus. I, J, *Chondrus crispus* (L.) Stackh.; I, longitudinal section with young and J, transverse section with mature sporangia. *a*, apical cell; *c*, cover-cells; *co*, cortex; *m*, medulla; *t*, tetrasporangia. (A, E, F, K after Rosenvinge; G after Darbishire; the rest after Kylin.)

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branch. The auxiliary cells (*a*) are cut off from the mother-cells so as to lie near the carpogonia; although formed prior to fertilisation, they remain vegetative, unless sexual fusion occurs, and enlarge and acquire abundant contents only after that event ((42) p. 62, (392) p. 39). The

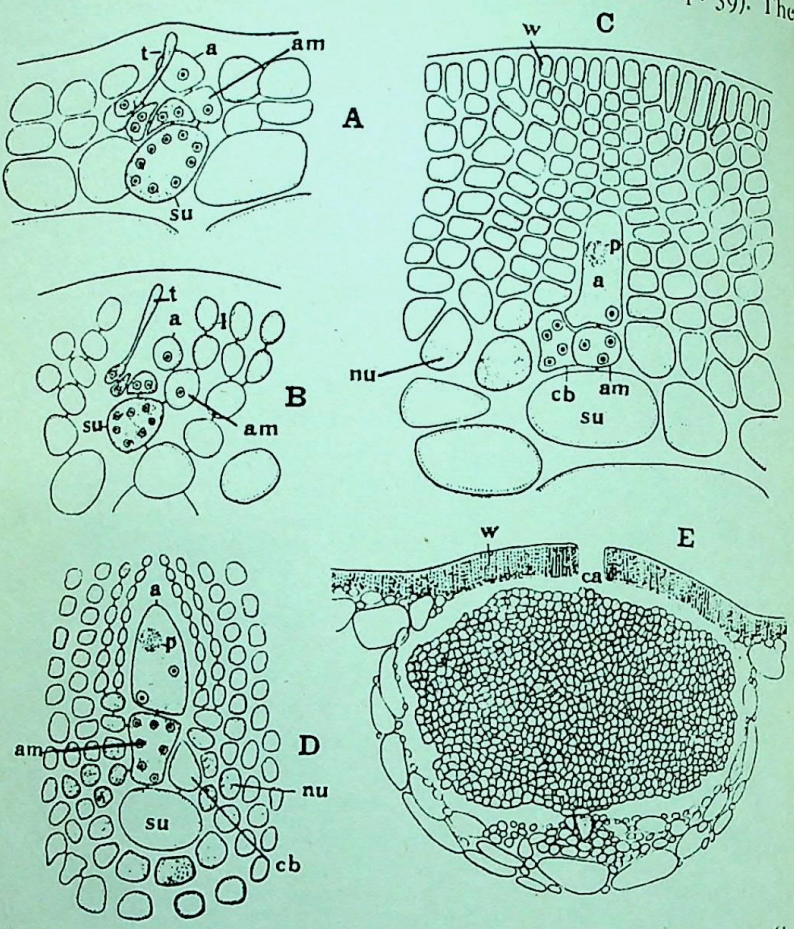

Fig. 264. A, C, *Rhodymenia pertusa* (Post. & Rupr.) J. Ag.; A, procarp, C, the same, some time after fertilisation. B, D, *Fauchea Fryeana* Setch.; B, procarp; D, the same, some time after fertilisation. E, *Chrysimenia* (*Botryocladia*) *pseudodichotoma* Farl., vertical section of fruit. *a*, auxiliary cell; *am*, auxiliary mother-cell; *ca*, carposporangia; *cb*, carpogonial branch; *l*, lateral; *nu*, nutritive tissue; *p*, protein-mass in auxiliary cell; *su*, supporting cell; *t*, trichogyne; *w*, wall of cystocarp. (E after Bliding; the rest after Kylin.)

gonimoblast-initial is cut off on the outer side of the auxiliary cell (fig. 266 F) and, during its further development, there is extensive fusion of cells; in the Champiaceae this is accompanied by great enlargement. Nutriment passes to the developing gonimoblast solely by way of the auxiliary mother-cell.

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Among Rhodymeniaceae *Rhodymenia pertusa* has been specially studied ((389) p. 36, (634) p. 31). The supporting cell (fig. 264 A, *su*) bears a three-celled carpogonial branch,[1] in addition to the auxiliary mother-cell (*am*). After fertilisation (fig. 264 C) the cells of the carpogonial branch (*cb*) fuse to form a multinucleate fusion-cell, which is displaced by the enlargement of the auxiliary cell (*a*) and of its now multinucleate mother-cell (*am*). The latter establishes pit-connections with the surrounding nutritive tissue (*nu*). At this stage the uninucleate auxiliary cell, as in other Rhodymeniales, contains a conspicuous round protein-mass (*p*). Meanwhile the overlying cells divide to form the wall (*w*) of the future cystocarp. The gonimoblast-initial gives rise to a mass of threads, in which most of the cells pro-

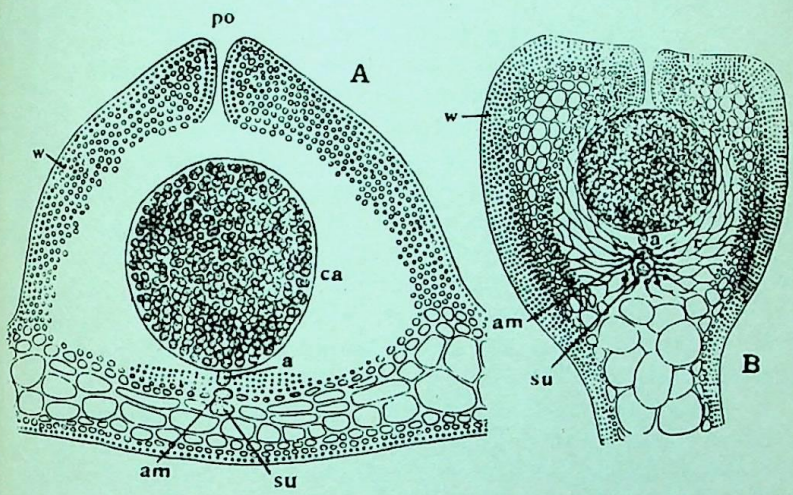

Fig. 265. Cystocarps of A, *Rhodymenia pertusa* (P. & R.) J. Ag. and B, *Fauchea Fryeana* Setch. *a*, auxiliary cell; *am*, auxiliary mother-cell; *ca*, carposporangia; *po*, aperture of cystocarp; *r*, reticulate tissue of cystocarp; *su*, supporting cell; *w*, wall of cystocarp. (After Kylin.)

duce small carpospores (fig. 265 A, *ca*). Within the swollen cystocarp (cf. also (90) p. 211, (94)) the mass of spores is separated by a wide space from the encompassing wall (*w*).

The antheridia of *R. palmata* ((87) p. 294, (169), (666) p. 225, (690) p. 22) form small irregular sori on the fronds. The colourless mother-cells arise by tangential division of the surface-cells and produce successively two primary and two secondary antheridia.

The procarps of *Fauchea* ((389) p. 33, (634) p. 25) and of *Botryocladia* (*Chrysimenia*) ((42) p. 53) are similar, but in the former (fig. 264 B) the auxiliary mother-cell (*am*) bears a short vegetative branch (*l*). The post-fertilisation events differ only in the fact (fig. 264 D) that, during the

[1] In *R. palmata* female plants are unknown and the carpogonia recorded by Grubb (257) are the hairs mentioned on p. 517 (cf. (169) p. 332, (634) p. 31).

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enlargement of the cystocarp in *Fauchea* (fig. 265 B), the inner cells of the pericarp stretch to form a reticulate tissue (*r*) surrounding the spores; this is so also in *Bindera*. In *Botryocladia* (fig. 264 E) the cystocarp projects into the hollow thallus (cf. also (364) p. 217, (778)). Some data about the antheridia are given by Kuckuck ((364) p. 213).

The Champiaceae differ only in matters of detail. The supporting cell (figs. 266 A, B; 267 A, *su*) is linked by a primary pit-connection to the cell of a longitudinal thread (*l*). The carpogonial branches (figs. 266 C; 267 A) are usually four-celled ((42) p. 44, (289) p. 347, (380) p. 44, (680) p. 26), commonly with the lowest cell transversely extended; they are three-celled in *Lomentaria* (fig. 266 A, B) and in *Champia lumbricalis* ((289) p. 341). In *Chylocladia* (fig. 266 C; (284) p. 74, (289) p. 330, (326) p. 133, (380) p. 40, (586) p. 223), *Gastroclonium* (fig. 266 D; (42) p. 28),[1] and not uncommonly in *Lomentaria clavellosa* (fig. 266 A), there are two auxiliary cells, though in the last only one undergoes further development. The product of fusion of the cells of the carpogonial branch (fig. 266 E, *f*) enlarges considerably, and in *Champia* (fig. 267 B; (42) p. 9, (289) p. 344)[2] a wide connection is established between it (*f*) and the supporting cell (*su*). The carpogonium connects with the auxiliary cell by a short thread (fig. 266 H, *c*), which may arise from the auxiliary cell (*Champia*, *Gastroclonium*), from the carpogonium, or from the fusion-cell; in *Lomentaria* there is not uncommonly a special connecting cell. The diploid nucleus divides within the carpogonium and one of the products passes into the auxiliary cell.

In *Chylocladia* and *Gastroclonium* (fig. 266 G) extensive fusions result in a large fusion-cell (*fu*) occupying the middle of the ripening cystocarp; these fusions involve not only the inner cells of the gonimoblast and the auxiliary cells, but the latter fuse with one another and with their mother-cells, as well as with some of the adjacent nutritive cells ((42) p. 30, (380) p. 41). In *Lomentaria* ((380) p. 47) and *Champia*, on the other hand, there is comparatively little fusion. In the former the richly branched gonimoblast gives rise successively to a number of gonimolobes in which most of the cells form carpospores (cf. Rhodymeniaceae), whereas in other Champiaceae (figs. 266 G; 267 E) the large carposporangia (*ca*) are terminal and develop simultaneously. In *Chylocladia* and *Gastroclonium* (fig. 266 F) the gonimoblast-initial divides by successive radial walls into wedge-shaped segments (*g*) which subsequently divide tangentially (fig. 266 G); the inner cells (*g*) fuse with the auxiliary cell, while the outer constitute the carposporangia (*ca*).

The cystocarp-wall begins to develop at the time of fertilisation by the outgrowth, from the cortical cells, of branched threads (figs. 266 E; 267 C, *w*), the cells of which become joined by secondary pit-

[1] As *Chylocladia ovalis*.

[2] Davis' (164) account of *Champia parvula* is erroneous.

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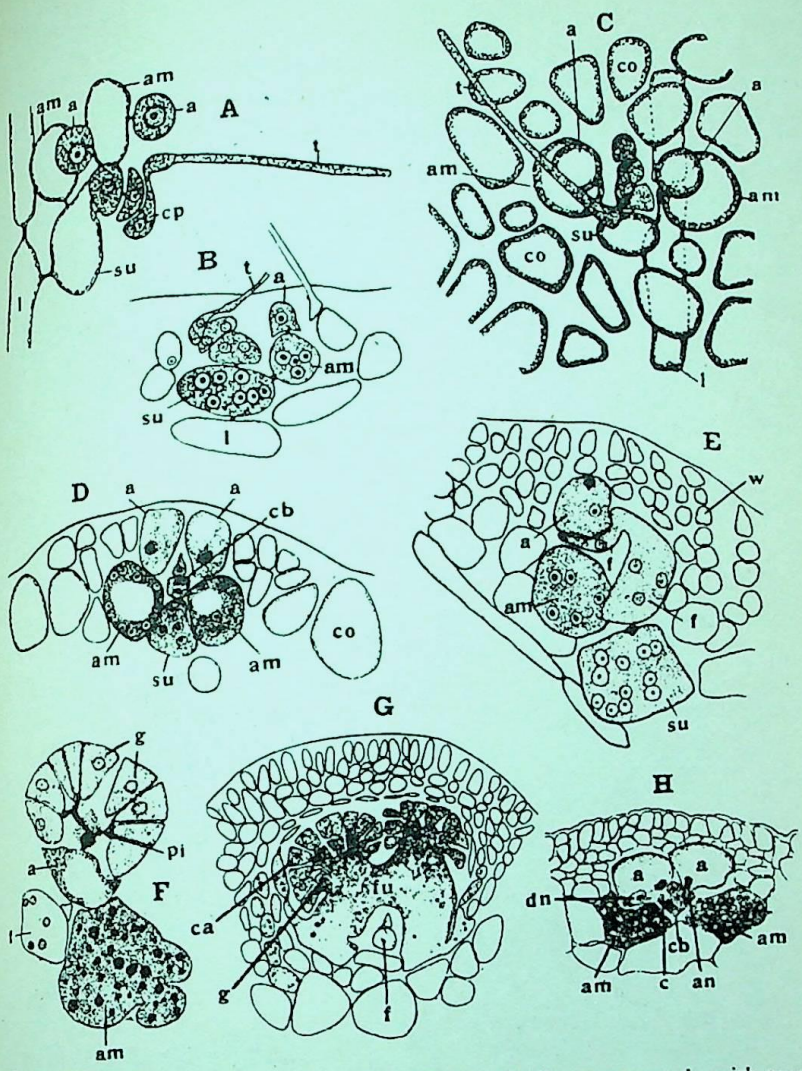

Fig. 266. A, B, *Lomentaria clavellosa* (Turn.) Gaill., procarps; A, with two and B, with one auxiliary cell. C, H, *Chylocladia kaliformis* (G. & W.) Hook.; C, procarp in surface-view of thallus; H, fusion between fusion-cell, formed from carpogonial branch (*cb*), and auxiliary cell. D, F, G, *Gastroclonium ovale* (Huds.) Kütz.; D, procarp after fertilisation; F, formation of gonimoblast; G, young cystocarp. E, *Lomentaria articulata* (Huds.) Lyngb., impending fusion between fusion-cell, formed from carpogonial branch (*f*), and auxiliary cell. *a*, auxiliary cell; *am*, auxiliary mother-cell; *an*, auxiliary cell nucleus; *c*, connecting filament; *ca*, carposporangia; *cb*, carpogonial branch; *co*, cortical cells; *cp*, carpogonium; *dn*, diploid nucleus; *f*, cell formed by fusion of cells of carpogonial branch; *fu*, composite fusion-cell; *g*, gonimoblast; *l*, cells of longitudinal threads; *pi*, pit-connection; *su*, supporting cell; *t*, trichogyne; *tc*, wall of cystocarp. (A, C after Kylin; H after Hassenkamp; the rest after Bliding.)

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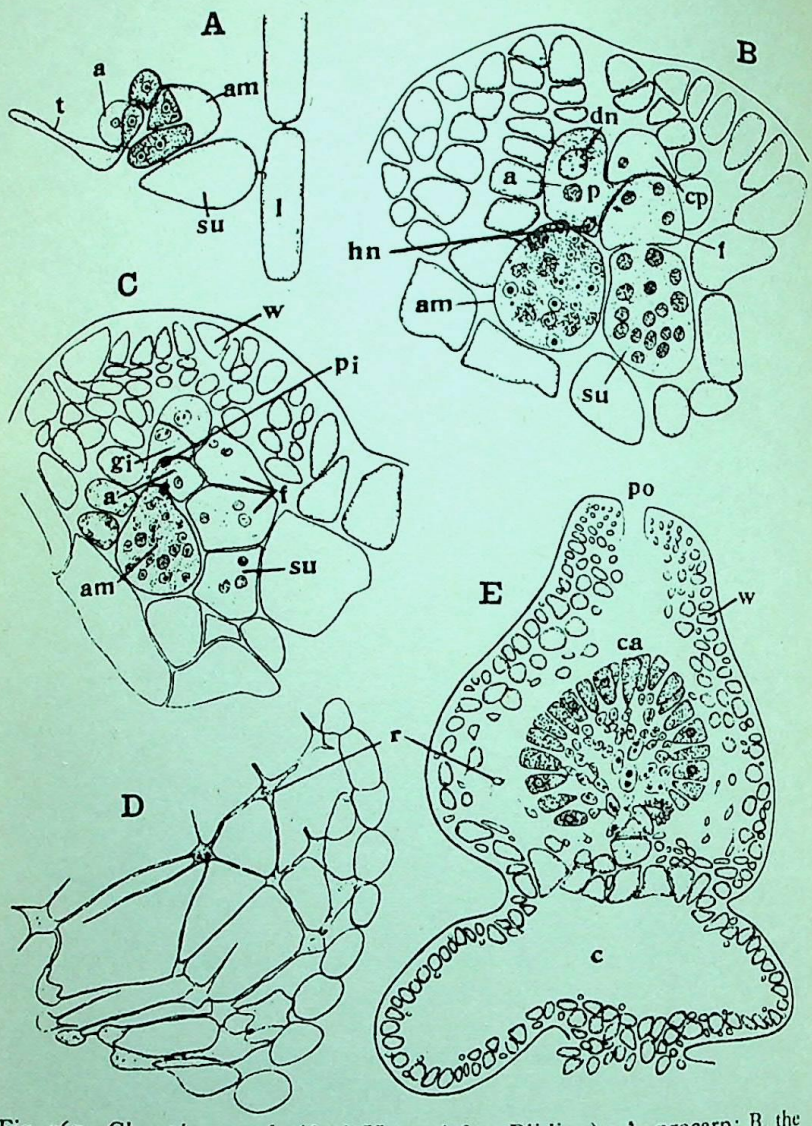

Fig. 267. *Champia parvula* (Ag.) Harv. (after Bliding). A, procarp; B, the same, some time after fertilisation; C, formation of gonimoblast-initial; D, part of reticulate tissue from a mature cystocarp; E, vertical section of cystocarp. *a*, auxiliary cell; *am*, auxiliary mother-cell; *c*, central cavity of thallus; *ca*, carposporangia; *cp*, carpogonium; *dn*, diploid nucleus; *f*, fusion-cell formed from the cells of the carpogonial branch; *gi*, gonimoblast-initial; *hn*, haploid nucleus; *l*, cell of longitudinal thread; *p*, protein-mass of auxiliary cell; *pi*, pit-connection; *po*, aperture of cystocarp; *r*, reticulate tissue of cystocarp; *su*, supporting cell; *t*, trichogyne; *w*, wall of cystocarp.

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connections. In *Champia*, and to a less marked extent in *Lomentaria*, the inner cells of the wall undergo considerable stretching during the enlargement of the cystocarp ((5) p. 125) and form a loose reticulate tissue (fig. 267 D, *r*) around the gonimoblast (cf. *Fauchea*). The cystocarps of *Chylocladia* and *Gastroclonium* are devoid of a pore.

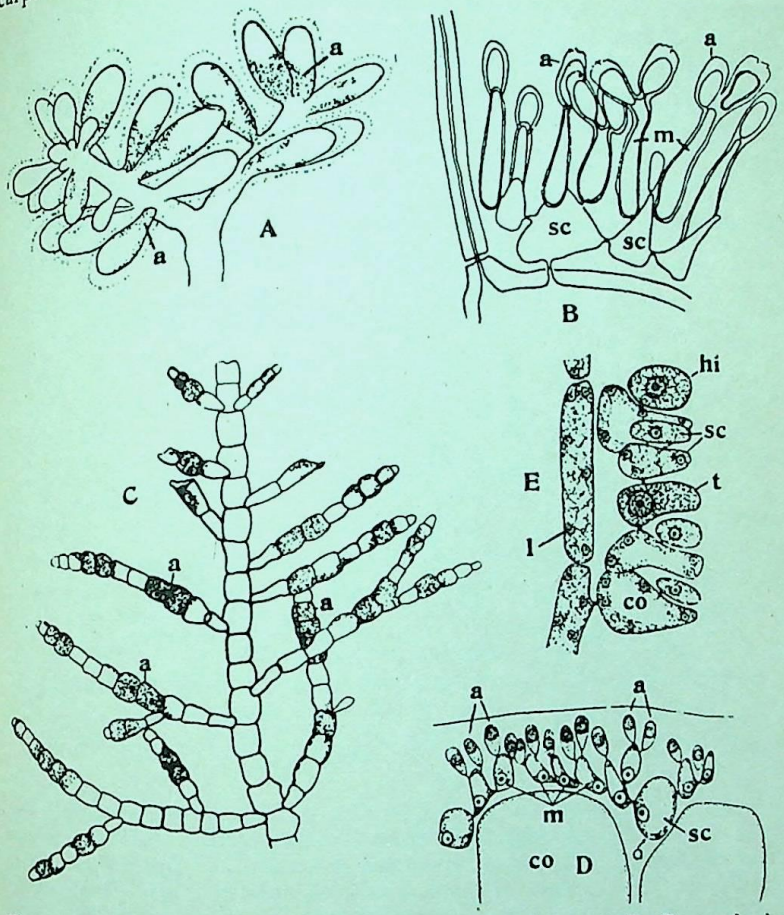

Fig. 268. Male plants and antheridia of Rhodymeniales. A, B, *Gastroclonium ovale* (Huds.) Kütz.; A, apex of a male plant; B, section through a male sorus. C, D, *Champia parvula* (Ag.) Harv.; C, habit of a male plant; D, section through a male sorus. E, *Chylocladia kaliformis* (G. & W.) Hook., developing tetrasporangia in longitudinal section. *a*, antheridial sori and antheridia; *co*, cortical cell; *hi*, hair-initial; *l*, cell of longitudinal thread; *m*, antheridial mother-cell; *sc*, secondary cortex; *t*, tetrasporangium. (D after Bliding; E after Kylin; the rest after Grubb.)

Bliding ((42) p. 65, (43)) is likely to be right in regarding *Lomentaria* as the least specialised member of the Champiaceae, the presence of two auxiliary cells being probably a secondary acquisition (cf. however (636)).

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Most Champiaceae are dioecious. The male sori of *Champia* ((42) p. 19, (50) p. 408, (258) p. 192, (486)) form girdle-shaped zones around the segments (fig. 268 C, *a*), while those of *Chylocladia* ((86) p. 249, (558) p. 580) encircle the furrows at the level of the diaphragms. In *Gastroclonium ovale* ((89) p. 185, (258) p. 187) they appear as white patches on the lower parts of the vesicles (fig. 268 A, *a*), while in *Lomentaria* ((85) p. 261, (87) p. 295, (380) p. 47, (558) p. 584)[1] they occupy the ultimate branches. The mother-cells (fig. 268 B, D, *m*) form a superficial network ((42) p. 19, (380) p. 47) resulting from anticlinal

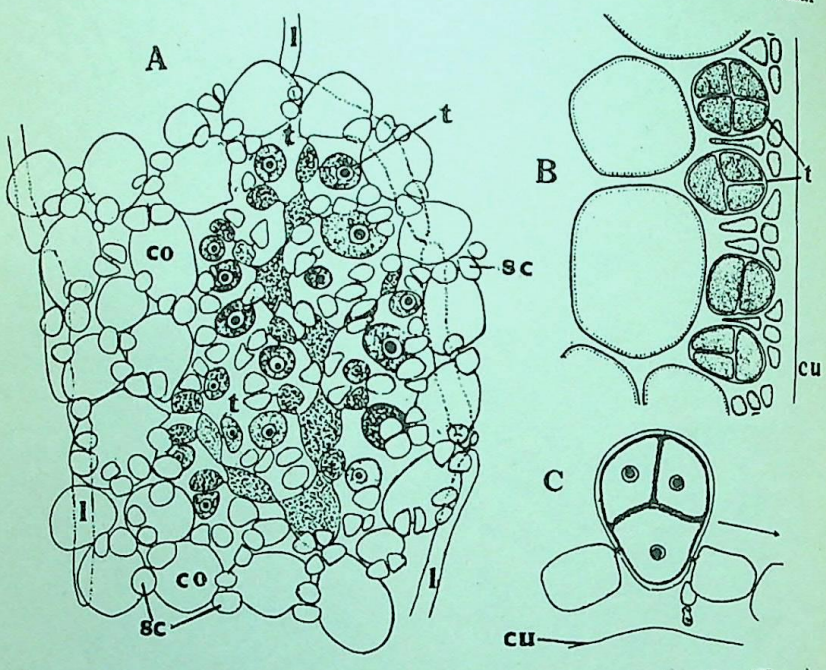

Fig. 269. Tetrasporangia of Rhodymeniales. A, *Lomentaria clavellosa* (Turn.) Gaill., developing sporangia, seen from the surface. B, *Rhodymenia pertusa* (Post. & Rupr.) J. Ag., mature sporangia in section. C, *Gastroclonium ovale* (Huds.) Kütz., the same. *co*, cortical cell; *cu*, cuticle; *l*, cell of longitudinal thread; *sc*, secondary cortex; *t*, tetrasporangia. (A, C after Bliding; B after Kylin.)

division of the secondary cortical cells (*sc*), although others ((258) pp. 190, 192, (558) p. 581) affirm that there are further divisions before the mother-cells are produced. Each mother-cell forms 2 or 3 antheridia (*a*).

(*b*) *The Tetrasporangiate Phase*

The usually cruciate tetrasporangia of Rhodymeniaceae lie amid the superficial tissues (fig. 269 B) and probably constitute end-cells of

[1] Webber's (718) antheridia are attaching organs ((42) p. 7).

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short laterals. In *Rhodymenia palmata* ((735) p. 158) they form irregular sori on both surfaces of the frond and originate from superficial cells which subsequently become embedded. Kuckuck (364) describes the sporangia of various species of the *Chrysimenia*-alliance. *Hymenocladia* (p. 744) has tetrahedrally divided sporangia formed from intercalary cells.

The large sporangia of Champiaceae ((42) pp. 21, 36, (380) p. 43) possess tetrahedral spores. They usually originate from uninucleate intercalary cells of the secondary cortex (figs. 268 E; 269 A, *t*), which enlarge so that they project into the central hollow (fig. 269 C). In *Lomentaria* ((42) p. 49, (380) p. 48, (392) p. 41, (411) p. 131, (680) p. 23), however, where the small sori occupy superficial depressions, the sporangia develop from the terminal cells of short branched laterals that arise from the primary cortical cells.[1]

7. The Diplobiontic Type among Ceramiales

This order, which was first separated from the Rhodymeniales of Schmitz (599) by Oltmanns ((500) p. 683) owing to its distinctive reproductive features, comprises the most specialised diplobiontic forms. Several of the peculiar characteristics were already noted by Phillips ((517) p. 201). Formation of the auxiliary cell in Ceramiales is deferred until after fertilisation (fig. 270 A, B), its mother-cell being the supporting cell (*su*) of the carpogonial branch (*cb*) which is, moreover, invariably a pericentral or (in Ceramiaceae) its equivalent.[2] The carpogonial branch represents a lateral borne upon the supporting cell and always consists of four cells devoid of laterals, although the supporting cell usually bears either one or two sterile branchlets. The uniformity of the sexual reproductive apparatus is as significant as the loss of all traces of heterotrichy in the early stages of development (p. 517).

(*a*) *The Sexual Phase*

(i) *Ceramiaceae.*

The members of this family, which probably represent the most primitive forms among Ceramiales ((380) p. 136, (387) p. 122), are distinguished by several characteristics. Communication between the fertilised carpogonium and auxiliary cell is usually established by means of special connecting cells (figs. 270 B; 272 H, *co*), no compact envelope is formed around the gonimoblast (figs. 270 E, F; 271 E; 272 J; 273 J), and most of the cells of the latter generally produce carpospores. The supporting cell of the procarp is homologous with

[1] The life-cycle of Rhodymeniales is discussed on p. 722.

[2] Schussnig ((604) p. 534) maintains that, in *Spermothamnion roseolum* and *Brongniartella byssoides*, the carpogonial branches arise direct from the fertile axis and that the auxiliary cell is already cut off prior to fertilisation.

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the fertile pericentral of other Ceramiales. The simplest condition is found in *Ballia* ((10) p. 27, (599) p. 497) and in most species of *Antithamnion*, where the branches (fig. 270 A, *sc*) bearing carpogonia on their basal cells do not differ from the other laterals of limited

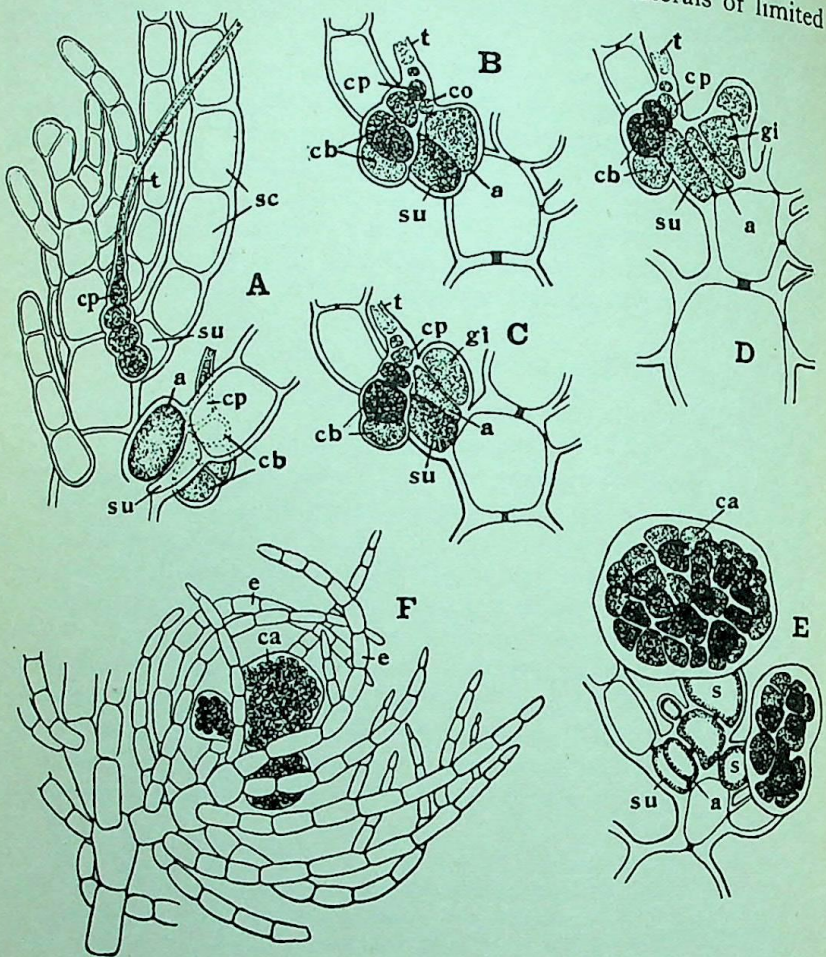

Fig. 270. *Antithamnion plumula* Thur. (after Kylin). A, branch-system with two carpogonial branches; B, procarp after fertilisation, formation of connecting cell (*co*); C, D, formation of gonimoblast-initial; E, groups of mature carposporangia; F, the same, with enveloping threads (*e*). *a*, auxiliary cell; *ca*, carposporangia; *cb*, carpogonial branch; *co*, connecting cell; *cp*, carpogonium; *gi*, gonimoblast-initial; *s*, sterile cells of gonimoblast; *sc*, sterile cells of fertile axis; *su*, supporting cell (auxiliary mother-cell); *t*, trichogyne.

growth; in *A. pacificum*, however, they are reduced to two or three cells ((150) p. 286,[1] (383) p. 48) and in *A. spirographidis* Schiffn. to two cells (739). In most other Ceramiaceae the fertile lateral is represented merely by the supporting cell and an overlying sterile cell, although

[1] As *A. floccosum*.

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the latter may later divide ((389) p. 85, (397) p. 19). The sterile cell (figs. 271 B; 272 B, C, *sc*) is cut off from the supporting cell prior to the development of the carpogonial branch (cf. however (180) p. 350). In *Crouania* ((389) p. 77) the single fertile member of a whorl is always much reduced and sometimes represented only by the supporting cell, and this is invariably so in *Callithamnion* (fig. 273 A), where there are no sterile cells in the procarp.

In *Antithamnion plumula* ((380) p. 61, (518) p. 356, (558) p. 366, (586) p. 236) the carpogonial branch arises from the under side of the basal cell (fig. 270 A, *su*) of the lateral and, at first, the supporting cell does not differ in any way from the others (*sc*); after fertilisation an auxiliary cell with dense contents (*a*) is cut off on the upper side. The fertilised carpogonium (fig. 270 B, *cp*) cuts off a small connecting cell (*co*) which fuses with the auxiliary cell (*a*). The gonimoblast-initial (fig. 270 C, D, *gi*) originates from the upper side of the latter and gives rise to several tufts of threads (fig. 270 E), in which the basal cell (*s*) remains sterile, while the remainder develop into carposporangia. The latter constitute several distinct groups (gonimolobes, fig. 270 F) and are surrounded by a loose envelope (*e*) formed from neighbouring sterile branches; in *A. pacificum* ((150) p. 287) and *A. spirographidis* (739) the gonimolobes ripen successively. Diverse investigators record fusions at the base of the gonimoblast ((93) p. 376, (150) p. 287, (518) p. 357). *Platythamnion villosum* ((150) p. 288, (380) p. 51) shows similar features. The cystocarps of *Ballia* occur in the axils of the fertile laterals.

The procarps of *Ceramium* ((326) p. 120, (380) p. 63, (456), (518) p. 361, (558) p. 372) develop just behind the apices. The supporting cell is the first-formed pericentral of a segment and commonly bears two carpogonial branches, although in *C. rubrum* there is only one. Two carpogonial branches are also met with in the closely related *Microcladia glandulosa* ((68) p. 15, (460) p. 292). The post-fertilisation development of *Ceramium* does not differ in any important detail from *Antithamnion*.

In *Wrangelia penicillata* ((69) p. 183, (386), (766) p. 381) the procarps arise on special distichous laterals of limited growth, which are crowded together at the apices of the main thallus-branches; in these fertile laterals (fig. 271 A–C) the pericentrals of the upper 10–15 segments produce whorls of branchlets consisting of only 2–3 cells. The slightly enlarged basal cell of the oldest member of each whorl (*su*), in the middle segments, bears a curved carpogonial branch (*1*, *2*, *3*), while the cells above (*sc*) are sterile; usually only one carpogonium on each lateral is fertilised. After fertilisation (fig. 271 E) all the branchlets (*l*) of the fertile lateral develop further and form a dense group overtopped by surrounding sterile branches (*e*). The gonimoblast-threads (fig. 271 E, *g*) spread over the axial cells (*a*) of the fertile branch and establish secondary pit-connections with the lower cells of the sterile laterals (*l*). The large terminal carposporangia (*ca*) are formed on branches of the

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creeping gonimoblast. The single cystocarp (fig. 271 E), produced from a fertile lateral, is traversed by the axial cells (*a*) and is provided with an incomplete, though relatively compact, envelope formed by the sterile laterals (*l*).

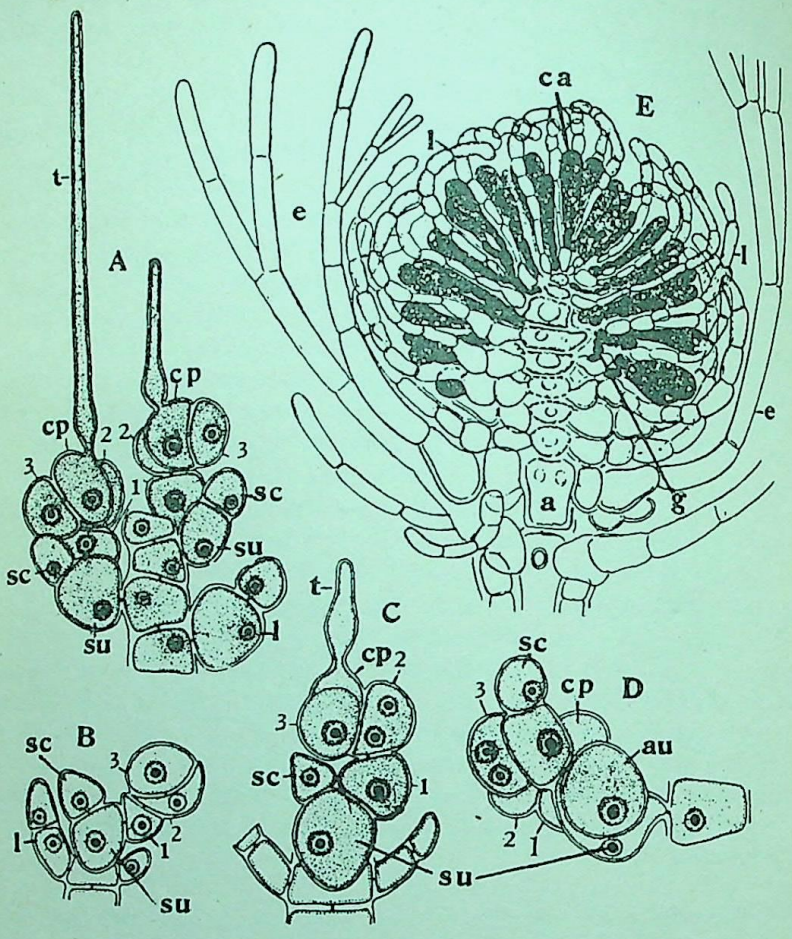

Fig. 271. *Wrangelia penicillata* C. Ag. A, apex of fertile branch with two carpogonia, the successive cells of the carpogonial branches numbered; B, young and C, mature procarp; D, formation of auxiliary cell; E, vertical section of mature cystocarp. *a*, axial cell; *au*, auxiliary cell; *ca*, carposporangia; *cp*, carpogonium; *e*, enveloping threads; *g*, gonimoblast; *l*, lateral; *sc*, sterile cell; *su*, supporting cell; *t*, trichogyne. (E after Bornet and Thuret; the rest after Kylin.)

The fertile branchlets of *Griffithsia*[1] (fig. 272 A, B, *fb*), which consist of a few multinucleate cells (3 in *G. corallina*; 5 in *G. setacea*), arise from the apices of the large axial cells (*a*), although soon deflected by

[1] See (193) p. 132, (326) p. 122, (375), (383) p. 58, (428) p. 656, (478) p. 396, (518) p. 357, (586) p. 236, (638) p. 58, (647).

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the development of a lateral. The lowest cell of the branchlet (fig. 272 C, *1*) later gives rise to the envelope of the cystocarp, while the subterminal one (*2*) produces the procarp. This cuts off three (usually only two in *G. globifera*) uninucleate pericentrals (cf. *Spermothamnion* and *Compsothamnion*), those to the right and left developing into two-celled branchlets (*su*, *sc*), the basal cell of which bears a carpogonial branch (cf. also fig. 272 B). There is direct fusion between the auxiliary cell[1] and the carpogonium; a special connecting cell is not produced. The auxiliary cell (fig. 272 D, *au*) produces several gonimoblast-initials (*gi*) which develop successively into richly branched gonimolobes, most of the cells of which give rise to uninucleate carpospores in basipetal sequence. Meanwhile there is considerable enlargement of the pit-connections (*pi*) between the cells of the fertile branchlet (*1–3*), while the sterile cell (*sc*) and supporting cell (*su*) fuse with one another and with the axis (*2*, *3*) of the branchlet (cf. also (442) p. 382); later the auxiliary cell (*au*) fuses with the supporting cell. The few enveloping threads (*e*) consist of only two cells. The ripe fruits, either sessile (*G. corallina*) or borne on short branchlets, are situated between the large cells of the thallus. Similar cystocarps occur in *Halurus* ((478) p. 399) and *Bornetia* ((691) p. 158).

In recent years the fruit-development of *Spermothamnion roseolum* has been repeatedly investigated.[2] The procarps (fig. 272 E, F) are produced on short laterals occupying the lower portions of the side-branches. The three upper cells (*1–3*) of these laterals possess dense contents and, as in *Griffithsia*, the subterminal one cuts off three pericentrals; the first, which subsequently degenerates, is formed abaxially (*p* in fig. 272 F), the others on the right and left flanks respectively (*p* and *su* in fig. 272 E; *su* in F). One of the latter constitutes the supporting cell (*su*) of the carpogonial branch and produces a single sterile cell (*sc*); the carpogonial branch (fig. 272 F, *cb*) curves towards the adaxial side of the fertile lateral. The entire procarp is enveloped in mucilage (*m*).

After fertilisation both of the last-formed pericentrals (one the supporting cell of the carpogonial branch, fig. 272 G, H, *su*) cut off auxiliary cells (*au*). The carpogonium (fig. 272 H, *cp*) puts out processes (*co*) which become cut off as connecting cells and fuse with the auxiliary cells; according to Drew ((176) p. 562, (179) p. 472) the zygote-nucleus divides twice and products enter the respective connecting cells. Some investigators ((558) p. 303, (606) p. 239) record

[1] Lewis' statement (cf. also (50) p. 207) that in *G. globifera* the supporting cell itself acts as the auxiliary cell remains doubtful.

[2] Kylin ((380) p. 53) and Schussnig ((606) p. 236) differ in their interpretation of the procarp (cf. also (387) p. 79, (389) p. 60, (558) p. 302, (603), (604) p. 534 and footnote 2 on p. 683); that of the former, which is supported by Drew and others ((176) p. 568, (179) p. 471, (460) p. 283) is adopted here. The data in the older literature ((68) p. 28, (326) p. 115, (478) p. 348, (500) p. 705, (531) p. 27) are only in part correct.

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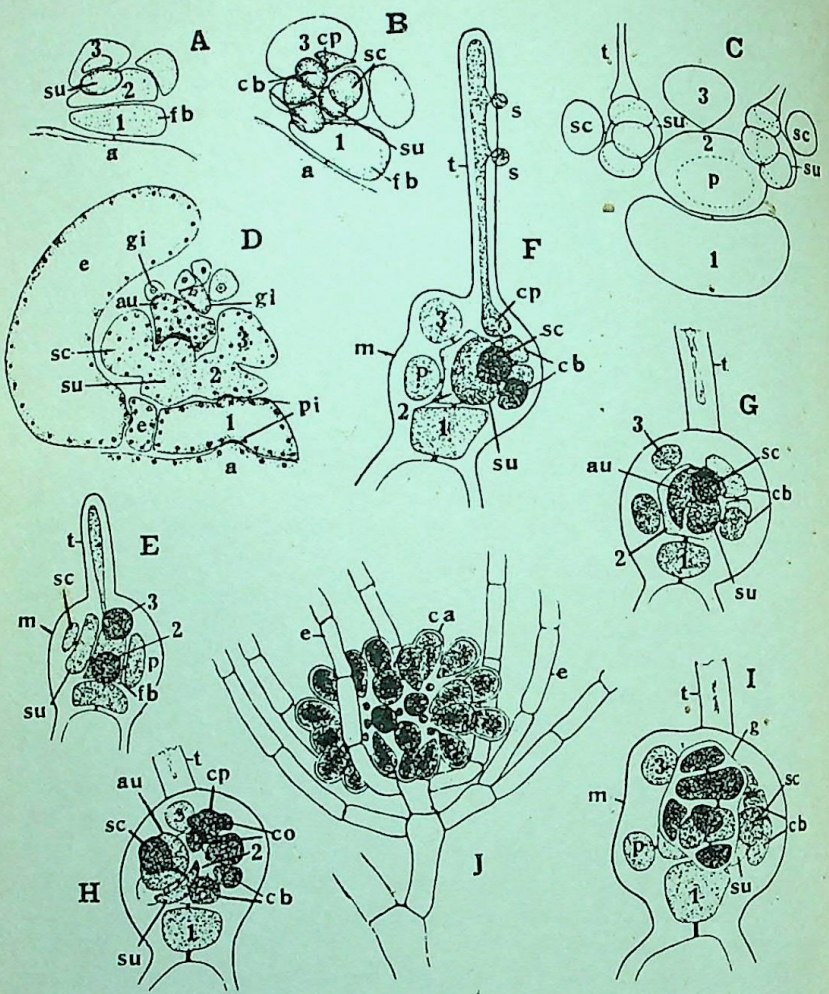

Fig. 272. A–D, *Griffithsia corallina* (Lightf.) Ag.; A, early development of carpogonial branch; B, almost mature procarp; C, diagram of fertile axis, with two procarps; D, post-fertilisation fusions and formation of gonimoblast-initials (*1–3* in A–D the three cells of the fertile axis). E–J, *Spermothamnion roseolum* (Ag.) Pringsh.; E, young procarp seen from the abaxial side; F, procarp at time of fertilisation seen from the flank; G, formation of auxiliary cell; H, formation of connecting cells (*co*); I, development of gonimoblast; J, mature gonimoblast (*1–3* in E–I the cells of the fertile axis). *a*, axial cell; *au*, auxiliary cell; *ca*, carposporangia; *cb*, carpogonial branch; *co*, connecting cells; *cp*, carpogonium; *e*, enveloping threads; *fb*, fertile branch; *g*, gonimo-blast; *gi*, gonimoblast-initial; *m*, mucilage-envelope; *p*, pericentral; *pi*, pit-connections; *s*, spermatium; *sc*, sterile cell; *su*, supporting cell; *t*, trichogyne. (After Kylin.)

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fusions between the cells of the carpogonial branch. The auxiliary cells divide transversely into four (fig. 272 I, *g*) and each segment produces several laterals forming terminal carposporangia (fig. 272 J, *ca*). The products of the two gonimoblasts usually combine to form a single fruit which is surrounded by a few sterile threads (*e*), arising from the lower cells of the fertile branchlet.

In *Callithamnion*[1] the procarp (fig. 273 A) normally includes two auxiliary mother-cells (pericentrals), only one of which (*su*) bears the curved carpogonial branch (*cb*); the other (*m*) is sometimes wanting. The carpogonium (*cp*) lies about midway between the two mother-cells, each of which (fig. 273 B, I) produces an auxiliary cell (*a*). The fertilised carpogonium (fig. 273 C, I) broadens and divides longitudinally into two cells (*co*). Each of these cuts off a small connecting cell (figs. 224 E, *co*; 273 B, *cc*) which fuses with a slight protuberance (fig. 273 C, D) from the adjacent auxiliary cell (*a*); there is considerable resemblance to the mode of formation of a secondary pit-connection. The nucleus of the auxiliary cell (*an*) takes up a basal position, while one of the two diploid nuclei (*dn*) travels to the apex of the auxiliary cell, meanwhile undergoing considerable enlargement. The degenerating auxiliary nucleus (figs. 224 F, *hn*; 273 E, *an*) and the other diploid nucleus (*dn*) are cut off by a basal septum, while the gonimoblast (fig. 273 F, *g*) arises from the apex of the auxiliary cell. The naked masses of carposporangia are either spherical (*C. corymbosum*, fig. 273 J) or composed of a number of successively maturing lobes (*C. Furcellarieae* (374)). In *Seirospora Griffithsiana* ((50) p. 224, (460) p. 284, (590) p. 116), with similar procarps, the gonimoblasts are loosely branched.

The procarps of *Ptilota plumosa* ((380) p. 59, (518) p. 362)[2] are again borne on short laterals in which the subterminal cell produces three pericentrals, but here the carpogonial branch arises from the first-formed abaxial one (fig. 274 A). The details are difficult to decipher owing to the outgrowth of all three pericentrals, as well as of the terminal cell of the fertile lateral, into sterile branchlets ending in elongate unicellular hairs (*h*). The fertilised carpogonium (fig. 274 B, *cp*) forms a special connecting cell (*co*) which fuses with the auxiliary cell (*a*). The procarps of *Plumaria elegans* ((180) p. 350, (518) p. 362, (660) p. 3) show no important differences.

The fertile pinnae of *Compsothamnion* ((737) p. 357) develop their procarps (fig. 273 G) in the same way, the subterminal cells successively producing three pericentrals (*p1*, *su*, *p3*), each of which generally bears a sterile cell (*sc*). The second and third pericentrals constitute auxiliary mother-cells and the former produces the carpogonial branch. The

[1] See (380) p. 56, (425) p. 117, (461) p. 179, (499) p. 115, (558) p. 316, (586) p. 236, (590) p. 115, (733) p. 135, (734) p. 164, (736) p. 197. The older accounts ((67) p. 145, (68) p. 32, (326) p. 117, (692) p. 69) are not altogether correct in matters of detail.

[2] Davis' account ((163) p. 356) of *P. serrata* is erroneous.

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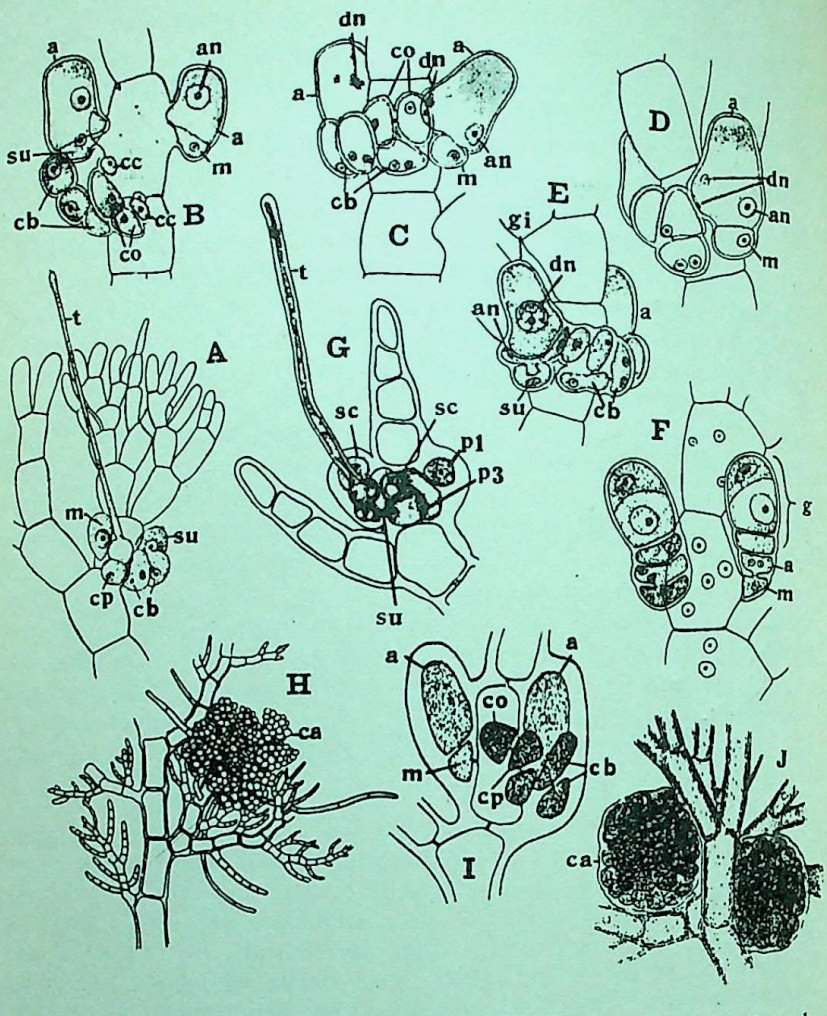

Fig. 273. A–F, J, *Callithamnion corymbosum* (Smith) C. Ag.; A, branch-system with young procarp; B, formation of auxiliary and connecting cells, the parts somewhat displaced; C, D, fusion of the two; E, formation of gonimoblast-initial; F, later development of gonimoblast; J, mature gonimoblasts. G, H, *Compsothamnion thuyoides* (Smith) Schmitz; G, young procarp; H, mature gonimoblast. I, *Callithamnion Furcellariae* J. Ag., formation of auxiliary and connecting cells. *a*, auxiliary cell; *an*, auxiliary cell nucleus; *ca*, carposporangia; *cb*, carpogonial branch; *cc*, connecting cells; *co*, the two cells into which the fertilised carpogonium divides; *cp*, carpogonium; *dn*, diploid nucleus; *g*, gonimoblast; *gi*, gonimoblast-initial; *m*, auxiliary mother-cell; *p*, pericentral; *sc*, sterile cells; *su*, supporting cell; *t*, trichogyne. (G, H after Westbrook; I after Kylin; J after Thuret and Bornet; the rest after Oltmanns.)

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naked fruits (fig. 273 H) are lobed. The sterile cells cut off from the second and third pericentrals, after further division, usually produce hyphae which establish pit-connections with the cells of adjacent laterals.

Ptilothamnion ((69) p. 179, (387) p. 77) is essentially like *Spermothamnion*, although the procarps are usually produced at the tips of longer branches and a single auxiliary cell is the rule. *Sphondylothamnion* ((69) p. 180, (458) p. 189) also has similar procarps.

Those of *Spyridia* ((520) p. 552) are formed on adventitious laterals (fig. 274 C), which consist of alternating sterile (*s*) and fertile (*f*) segments. The latter produce procarps alternately to right and left, the fertile segment forming four pericentrals (*p*), one of which (*su*) bears the carpogonial branch. Growth in length of the axis is terminated by the fertilisation of a procarp. The first of the several pericentrals of each sterile segment gives rise to a "filament" (*fi*), while the others, as well as the pericentrals of fertile segments whose procarp fails to develop further, grow out into richly branched threads (fig. 274 E, *e*). The other changes occurring after fertilisation are obscure and require further investigation. According to Phillips ((520) p. 555) there are three gonimoblasts (fig. 274 D, E, *g*) which arise from cells (*sa*) cut off from the three remaining pericentrals (*p*) of the fructifying segment; these cells are stated to put out processes (fig. 274 E) which fuse with the large auxiliary cell (*a*)—a very unusual state of affairs. Many of the gonimoblast-cells produce carpospores. The entire fertile branch (cf. *Wrangelia*) gives rise to a three-lobed fruit and the carposporangia are embedded amid the sterile threads described above (cf. fig. 274 E); only the basal parts of the "filaments" persist.

Kylin ((389) p. 76) distinguishes among Ceramiaceae two series, viz. (*a*) *Crouania*, *Antithamnion*, *Platythamnion*, *Ceramium*, *Wrangelia*, in which the branches bearing procarps are homologous with vegetative laterals of limited growth, and (*b*) *Griffithsia*, *Spermothamnion*, *Ptilota*, *Callithamnion*, in which vegetative laterals of limited growth, comparable to those which bear the procarps, are lacking. In the second series the fertile laterals are always reduced to a few cells. The vegetative laterals, seen in *Griffithsia*, *Sphondylothamnion*, and *Halurus*, are regarded as secondary in origin and not as homologous with those of a *Crouania* or *Antithamnion*. This point of view is justified by a comparison of the mode of origin of the procarps in the different genera.

Most Ceramiaceae are dioecious and the male plants are frequently smaller than the female; *Spermothamnion* and certain *Ceramiums* are usually monoecious. The antheridia commonly form dense clusters (fig. 275 C, H, *a*) on branchlets that arise for the most part from the upper sides of the laterals, as in *Antithamnion plumula* ((93) p. 374, (558) p. 365), *Spermothamnion* ((179) p. 470, (558) p. 301, (606) p. 230) and *Compsothamnion* ((89) p. 185, (737) p. 356). One or two of the basal cells of the branchlet are generally sterile (fig. 275 I, K, *s*), while the mother-

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cells (*m*) arise by periclinal division of the remainder. The sori of *Callithamnion*[1] (fig. 275 G) constitute spherical or cushion-like groups,

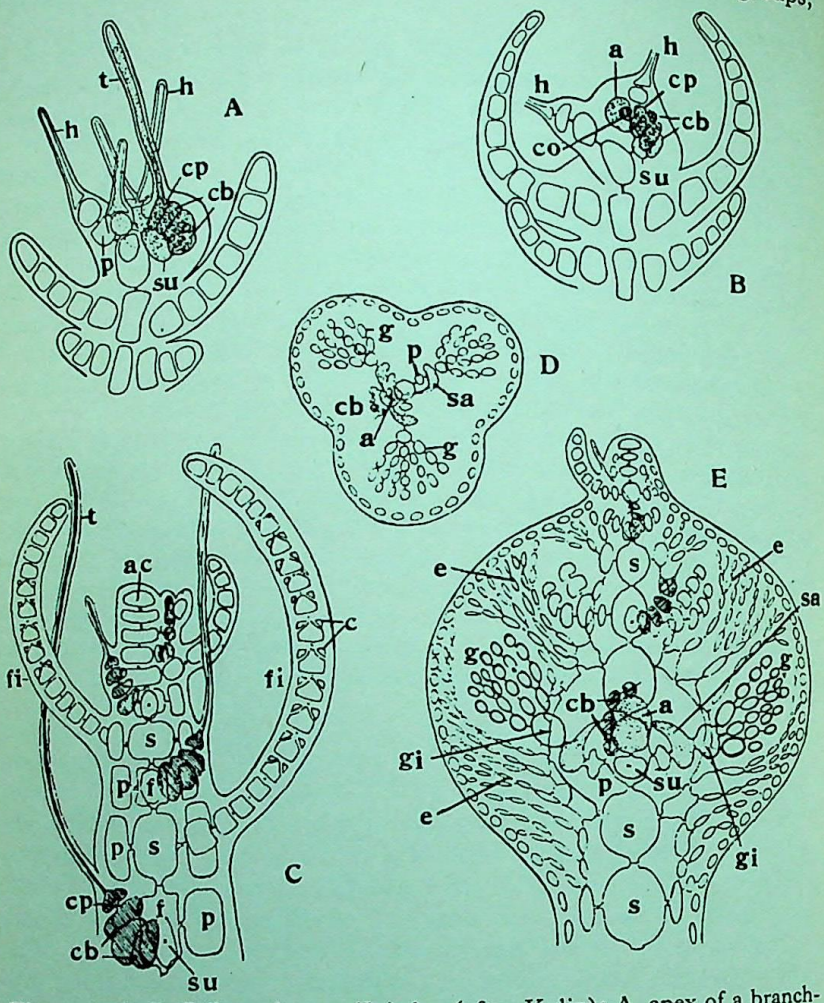

Fig. 274. A, B, *Ptilota plumosa* (L.) Ag. (after Kylin); A, apex of a branch-system with hairs and a young procarp; B, formation of auxiliary and connecting cells. C–E, *Spyridia filamentosa* (Wulf.) Harv. (after Phillips); C, part of a lateral bearing procarps; D, transverse and E, longitudinal sections of a developing cystocarp. *a*, auxiliary cell; *ac*, apical cell; *c*, cortical cell; *cb*, carpogonial branch; *co*, connecting cell; *cp*, carpogonium; *e*, threads forming carpogonial branch; *f*, fertile axial cell; *fi*, "filament"; *g*, gonimoblast; *gi*, gonimoblast-envelope; *h*, hair; *p*, pericentral; *s*, sterile axial cell; *sa*, parent-cells of gonimoblasts; *su*, supporting cell; *t*, trichogyne.

enclosed in a common gelatinous sheath and composed of a dense mass of small-celled threads on which the mother-cells arise terminally. In

[1] See (85) p. 258, (258) p. 223, (453) p. 17, (558) p. 316, (692) p. 69, (733) p. 135, (734) p. 162, (736) p. 196.

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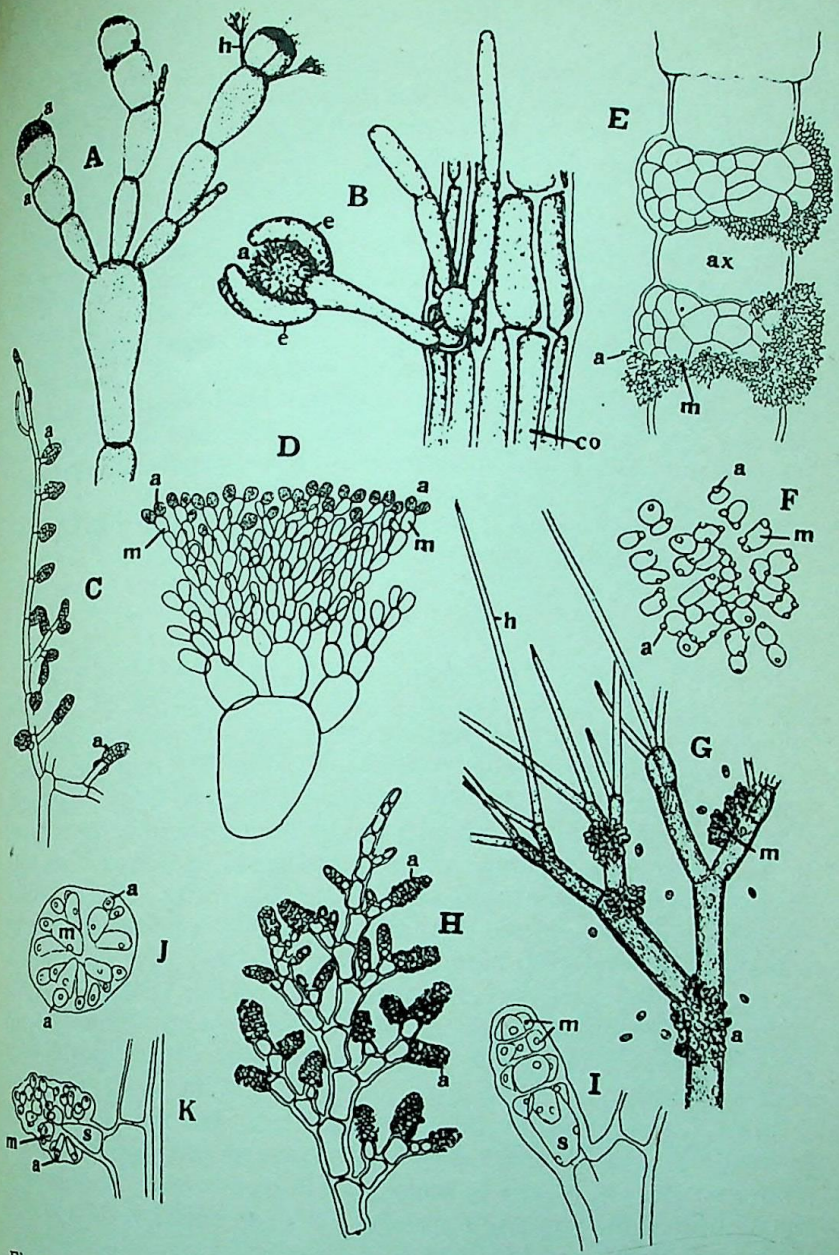

Fig. 275. Antheridia of Ceramiaceae. A, *Griffithsia globifera* (Harv.) J. Ag., tip of a male plant with antheridial sori (*a*). B, *Wrangelia penicillata* C. Ag., antheridial branch. C, I–K, *Spermothamnion repens* (Dillw.) Rosenv.; C, distribution of antheridial sori; I–K, a sorus enlarged, in J in cross-section. D, *Griffithsia corallina* (Lightf.) Ag., one of the antheridial branches composing a sorus. E, *Ceramium diaphanum* (Lightf.) Roth, two sori. F, *C. rubrum* (Huds.) C. Ag., surface view of small part of same. G, *Callithamnion corymbosum* (Smith) C. Ag. and H, *Compsothamnion thuyoides* (Smith) Schmitz, antheridial sori. *a*, antheridia or antheridial sori; *ax*, axial cell *co*, cortical threads; *e*, enveloping threads; *h*, hair; *m*, antheridial mother-cell *s*, stalk-cell. (A after Lewis; B after Boergesen; C, I–K after Rosenvinge D after Kylin; E after Taylor; F after Grubb; G after Thuret & Bornet H after Westbrook.

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Ptilota ((518) p. 365, (558) p. 357) and *Plumaria* ((86) p. 247, (180) p. 354) the antheridia cover the tips of the finer branches. The mother-cells in *Ceramium* ((84) p. 342, (85) p. 260, (258) p. 228, (513) pp. 50, 85) arise by division of the cells of the cortical bands (fig. 275 E, F), while in *Spyridia* ((85) p. 260, (520) p. 551) the greyish sori occupy the cortical bands of the "filaments".

The peculiar male heads of *Wrangelia* ((50) p. 121, (766) p. 380), simulating the conidiophore of an *Eurotium* (fig. 275 B), comprise numerous branchlets borne on the globular terminal cell and enveloped by several one-celled threads (*e*). The antheridial sori of *Griffithsia* ((258) p. 215, (375) p. 113, (638) p. 57, (692) p. 71), lastly, form caps on the terminal segments or encircle the constrictions between the younger cells (fig. 275 A, *a*); they consist of densely branched laterals (fig. 275 D) composed mainly of uninucleate cells. For the male sori of *Halurus* see (258) p. 220; for those of *Bornetia*, see (458) p. 192.

The mother-cells usually produce two or three antheridia (fig. 275 D, F; four in *Halurus*) and secondary antheridia are often formed.

(*ii*) *Delesseriaceae.*

Of the two groups of sterile cells, characteristic of the procarps of this family (figs. 277 A; 279 B, C, E), one (*s1*) is cut off from the supporting cell (*su*) before, and the other (*s2*) after, the formation of the initial of the carpogonial branch (*cb*). The first group is homologous with the sterile cells of Ceramiaceae and, as there, represents what is left of the fertile lateral bearing the carpogonial branch (cf. p. 684). The second group, on the other hand, is homologous with the carpogonial branch itself, since in *Polyneura* (fig. 281 C) and the Australian *Hemineura* ((382) p. 5) it is replaced by a second (*2*), though less strongly developed, carpogonial branch ((382) p. 36, (389) p. 85, (397) p. 17); according to Phillips ((519) p. 193) this is sometimes also so in *Apoglossum ruscifolium*. In the Delesserieae, by contrast to the Nitophylleae, the first set of sterile cells acquire dense contents only after fertilisation.

In all Delesserieae the procarps arise from the axial cells of the fertile fronds. In *Delesseria sanguinea*[1] these are constituted by minute lanceolate leaflets, arising in considerable numbers in autumn from the midribs of the vegetative fronds. Every axial cell of such a fertile leaflet, apart from a few of the apical segments which develop only lateral pericentrals (fig. 276 B, *p*), produces a pair of procarps (fig. 276 A). The first step in their development is the cutting off, in the plane of the frond, of tangential pericentrals (cf. fig. 279 D, *p*) which function as supporting cells (fig. 276 A, *su*). Each divides periclinally (fig. 276 E) to produce the first sterile cell (*sc*), after which the initial of the carpogonial branch (*cb*) is cut off by an anticlinal wall (cf. also fig. 279 E). The carpogonial branches usually arise alternately to right

[1] See (353) p. 42, (380) p. 95, (519) p. 175, (665) p. 275, (668).

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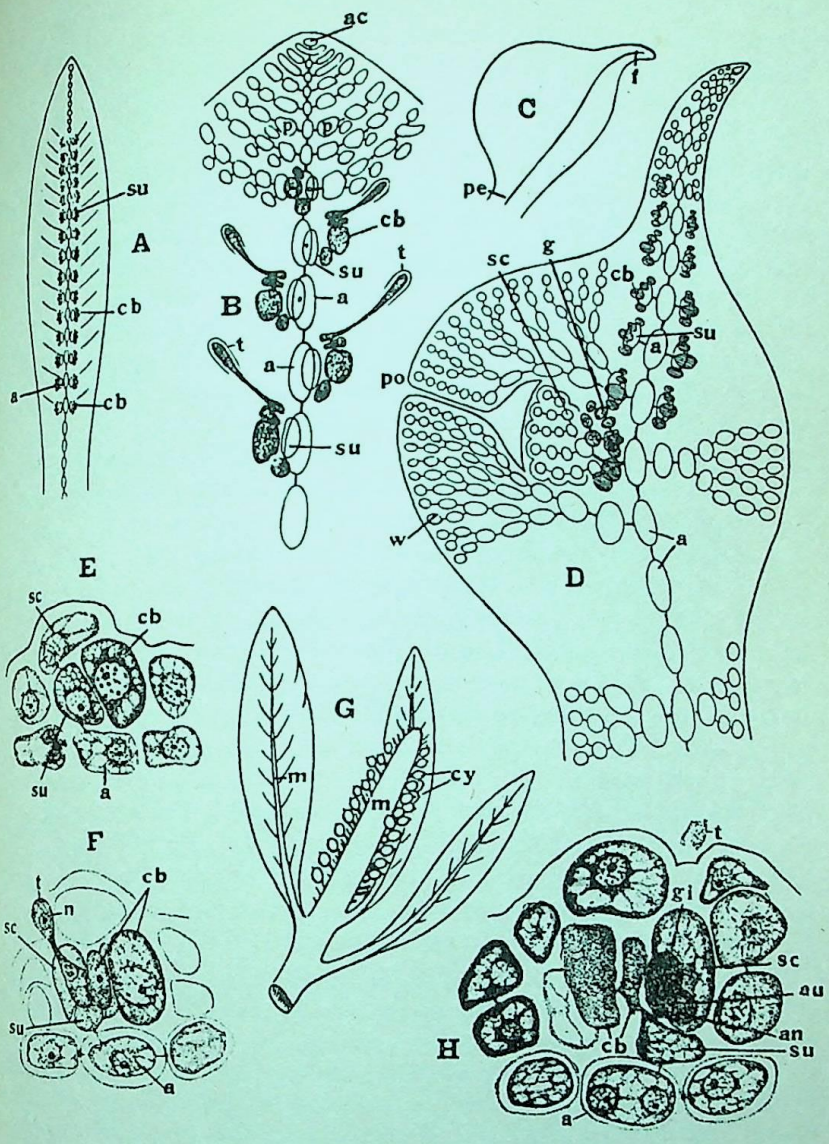

Fig. 276. *Delesseria sanguinea* Lamour.; A, side-view of fertile frond; B, part of a fertile frond in front view, greatly enlarged; C, outline of cystocarp, seen from the side; D, longitudinal section in a plane perpendicular to B, with developing cystocarp; E, developing procarp in section; F, procarp at time of fertilisation; G, cystocarps (*cy*) on midrib of frond of previous season; H, formation of gonimoblast-initial. *a*, axial cell; *ac*, apical cell; *an*, auxiliary cell nucleus; *au*, auxiliary cell; *cb*, carpogonial branch; *f*, tip of fertile frond; *g*, gonimoblast; *gi*, gonimoblast-initial; *m*, midrib; *n*, trichogyne nucleus; *p*, pericentral; *pe*, stalk of cystocarp; *po*, aperture of cystocarp; *sc*, sterile cell; *su*, supporting cell; *t*, trichogyne; *w*, wall of cystocarp. (E, F, H after Svedelius; the rest after Phillips.)

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and left in successive segments (fig. 276 B), the pair belonging to a given segment being mostly directed to the same side; the inflated trichogynes (*t*) project obliquely above the general surface. The second cell of the carpogonial branch is larger than the others (fig. 276 F). As many as 50 procarps may be formed in a fertile leaflet and, since they mature in acropetal succession, fertilisation is possible over a prolonged period. At about the time of fertilisation a second sterile cell (not visible in the figures) is cut off from the supporting cell and both sterile cells divide to form short threads (cf. fig. 279 F, G, *s1*, *s2*).

The entire fertile leaflet forms a single cystocarp and, as a general rule, probably only one procarp is fertilised. According to Phillips ((519) p. 180) its axial cell and the associated pericentrals, as well as the adjacent axial cells, acquire abundant contents so that they are readily picked out with a lens in a leaflet suitably stained. The lower cells of the carpogonial branches of the remaining procarps grow out into vegetative threads and help in the formation of the pericarp (fig. 276 D, *w*). The carpogonium fuses directly with the auxiliary cell of the fertilised procarp, while the gonimoblast-initial (fig. 276 H, *gi*) gives rise to a richly branched thread, in which many of the cells form carpospores. During these events the cells of the sterile threads (fig. 276 D, *sc*) have multiplied and acquired dense contents; later the cells disintegrate leaving a cavity which is occupied by the gonimoblast. The auxiliary cell fuses with the supporting and axial cells, as well as with some of the older gonimoblast cells, to form a large fusion-cell (cf. fig. 277 D, *f*), upon which the rows of carposporangia are borne. The mature cystocarps (fig. 276 C, G) are pedicellate (*pe*) and provided with an aperture (fig. 276 D, *po*); they constitute asymmetrical swellings (fig. 276 C), the surmounting flap (*f*) representing the apex of the fertile leaflet.

The arrangement and structure of the procarps (fig. 277 A, B) and the mode of production of the cystocarp (fig. 277 D) are essentially the same in *Membranoptera* ((380) p. 112, (519) p. 185), *Apoglossum* ((380) p. 87, (519) p. 188), and *Hypoglossum* ((382) p. 10, (519) p. 187), although here the procarps arise from the midribs of the ordinary vegetative fronds (figs. 189 D; 277 C). Similar cystocarps occur in *Caloglossa* ((146) p. 9).

In *Grinnellia* the procarps usually appear scattered (fig. 190 A, *cy*) as in Nitophylleae, but they actually arise ((382) p. 22)[1] from fertile leaflets (fig. 278 A, the shaded group) resembling those of a *Delesseria*, although completely embedded in the parent-thallus; the procarp arises from one of the axial cells (*a*) of such a leaflet. Occasionally the fertile expanses develop as leafy structures projecting above the surface (fig. 278 C, *f*) and within them a number of procarps may be formed; the resulting cystocarps then appear stalked (fig. 278 B, *cy*).

[1] See also the account of Brannon ((75) p. 14) which is, however, erroneous in certain respects.

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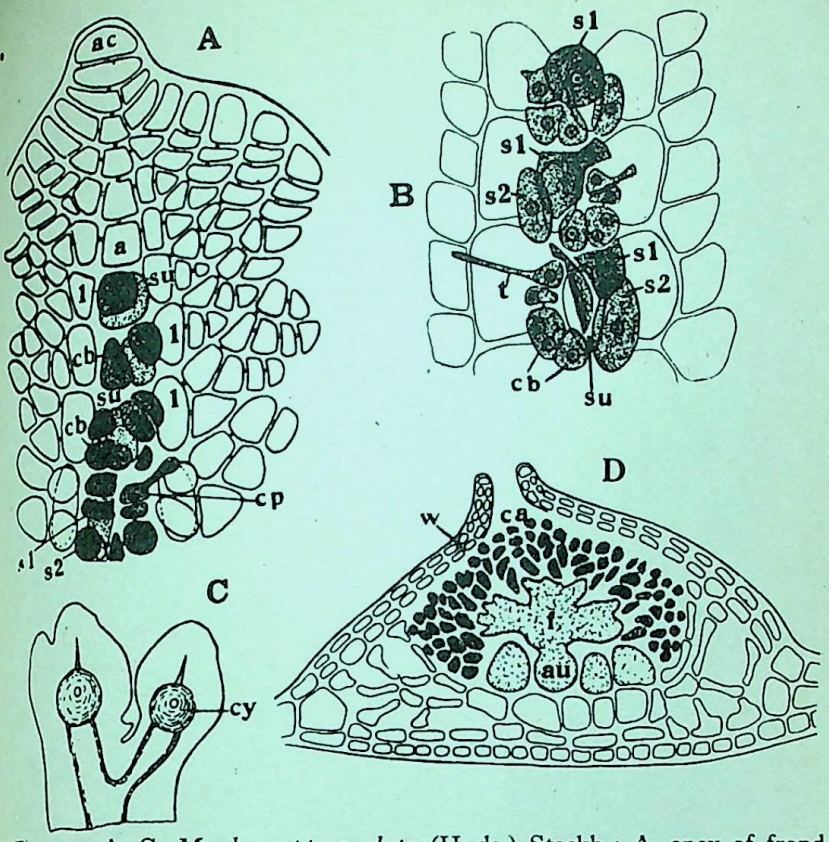

Fig. 277. A, C, *Membranoptera alata* (Huds.) Stackh.; A, apex of frond showing development of procarps, in surface-view; C, part of a frond, with two cystocarps (*cy*). B, D, *Hypoglossum Woodwardii* Kütz.; B, surface-view of part of frond, with developing procarps; D, transverse section of cystocarp. *a*, axial cell; *ac*, apical cell; *au*, auxiliary cell; *ca*, carposporangia; *cb*, carpogonial branch; *cp*, carpogonium; *f*, fusion-cell; *s1*, *s2*, sterile cells; *su*, supporting cell; *t*, trichogyne; *w*, wall of cystocarp: 1 (in A), the first-formed sterile cell (deeply shaded). (After Kylin.)

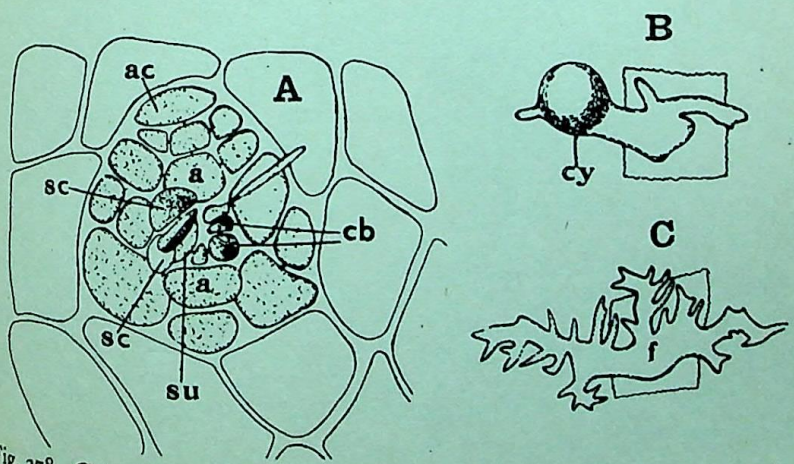

Fig. 278. *Grinnellia americana* (C. Ag.) Harv. (after Kylin). A, surface-view of fertile area, with procarp; B, cystocarp; C, specially developed fertile area. *a*, axial cell; *ac*, apical cell; *cb*, carpogonial branch; *cy*, cystocarp; *f*, fertile frond; *sc*, sterile cell; *su*, supporting cell.

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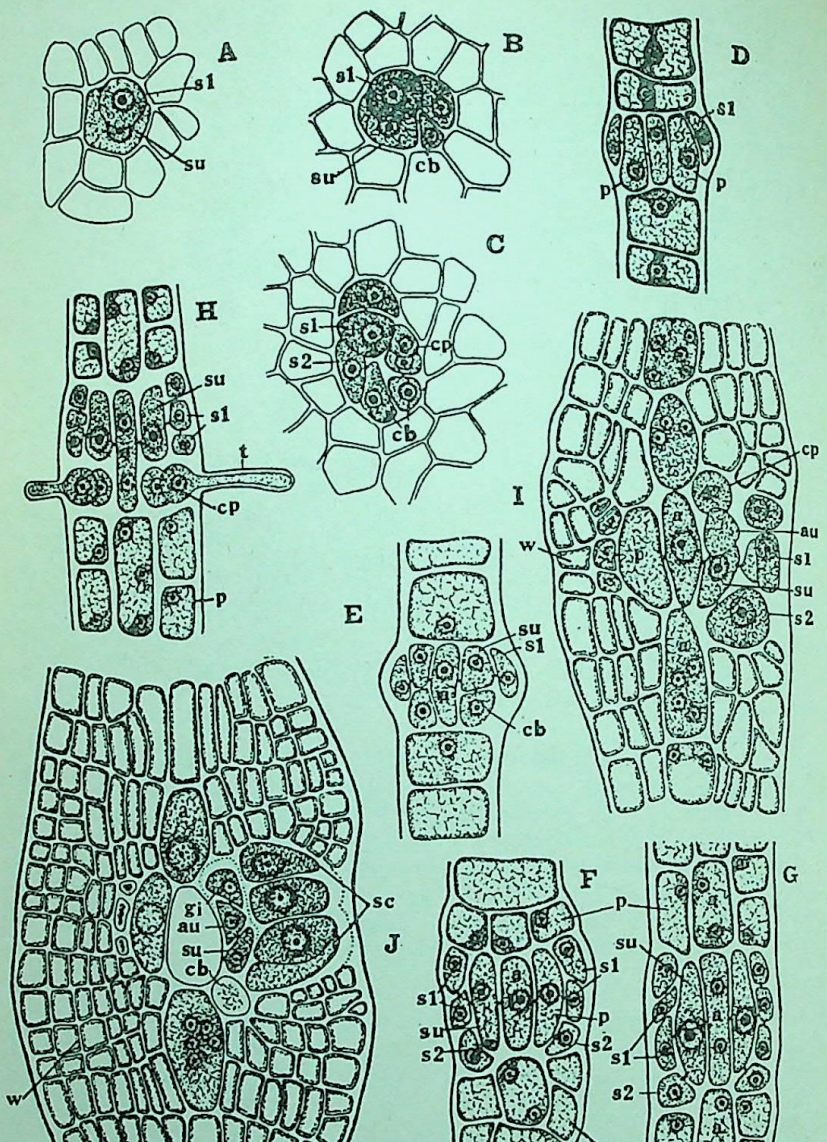

Fig. 279. *Phycodrys rubens* (Huds.) Batt. (after Kylin). A–C, successive stages in development of procarp, in surface-view; D–H, the same, in vertical sections of the frond; I, formation of auxiliary cell and nuclear division in carpogonium; J, formation of gonimoblast-initial. *a*, axial cell; *au*, auxiliary cell; *cb*, carpogonial branch; *cp*, carpogonium; *gi*, gonimoblast-initial; *p*, pericentral; *s1*, *s2*, *sc*, sterile cells; *su*, supporting cell; *t*, trichogyne; *w*, wall of cystocarp.

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The procarps of *Claudea* ((508) p. 21) and *Vanvoorstia* ((508) p. 43) arise from the dorsal pericentrals (p. 539). The single cystocarp, produced from each fertile frond, bears tooth-like projections on its lower surface representing daughter-blades which have failed to anastomose.

Phycodrys rubens ((357) p. 255, (380) p. 71, (519) p. 191), like other Nitophylleae, shows an irregular disposition of the procarps, which appear as white dots near the margins or on special marginal proliferations of the older fronds. The fertile cells, which are larger and have denser contents (fig. 279 A, *su*), cut off tangential pericentrals (fig. 279 D, *p*) which divide like those of *Delesseria* to form pairs of procarps (fig. 279 E–G), with the trichogynes standing perpendicular to the frond (fig. 279 H). The adjacent vegetative cells likewise cut

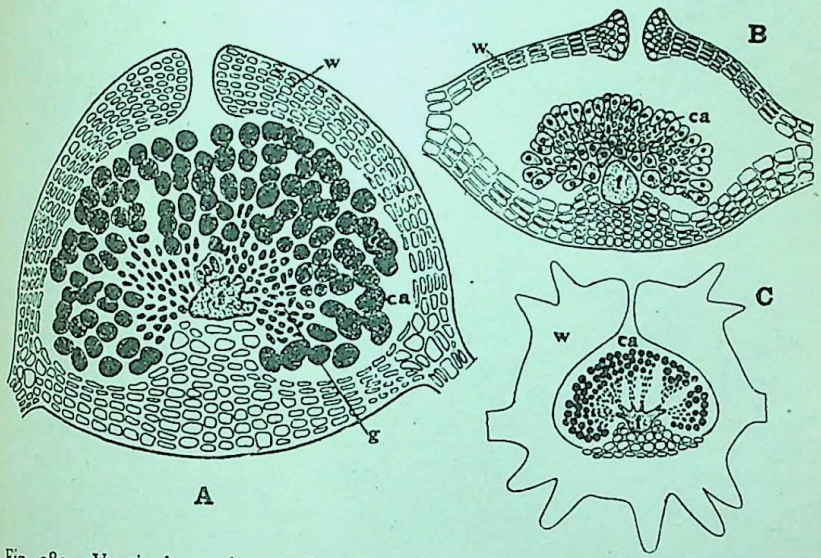

Fig. 280. Vertical sections of cystocarps of Nitophylleae (after Kylin). A, *Phycodrys rubens* (Huds.) Batt. B, *Nitophyllum punctatum* (Stackh.) Grev. C, *Polyneura Hilliae* (Grev.) Kyl. *ca*, carposporangia; *f*, fusion-cell; *g*, gonimoblast; *w*, wall of cystocarp.

off tangential pericentrals (fig. 279 F–H, *p*). Both sterile cells divide (fig. 279 F, G, *s1*, *s2*), the colourless elements thus formed overlying the supporting cell (*su*) and carpogonial branch.

After fertilisation (fig. 279 I), as the auxiliary cell (*au*) is cut off, nutritive materials accumulate in the axial (*a*) and adjacent cells, as well as in the two groups of sterile cells (*s1*, *s2*), while the latter lengthen at right angles to the surface (fig. 279 J). Simultaneously division of the surrounding pericentrals initiates the cystocarp-wall (*w*). The gonimoblast-initial (*gi*) segments vertically to form a small disc, the cells of which give rise to richly branched threads (fig. 280 A, *g*) in which 2–4 of the upper cells produce carpospores (*ca*). These threads radiate from a large fusion-cell (*f*) which is formed as in

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Delesseria. During the development of the gonimoblast the sterile (nutritive) cells disorganise, the resulting gap forming the aperture of the cystocarp.

Other Nitophylleae are essentially similar (cp. fig. 281 D with 279 J). In *Polyneura* ((382) p. 35, (519) p. 193),[1] as already noted above, the second group of sterile cells is replaced by a carpogonial branch (fig. 281 C, *2*) which is sometimes imperfect; in *Cryptopleura* (fig. 195 A, *p*; (382) p. 86, (442) p. 394, (519) p. 193)[1] the sterile groups (fig. 281 E,

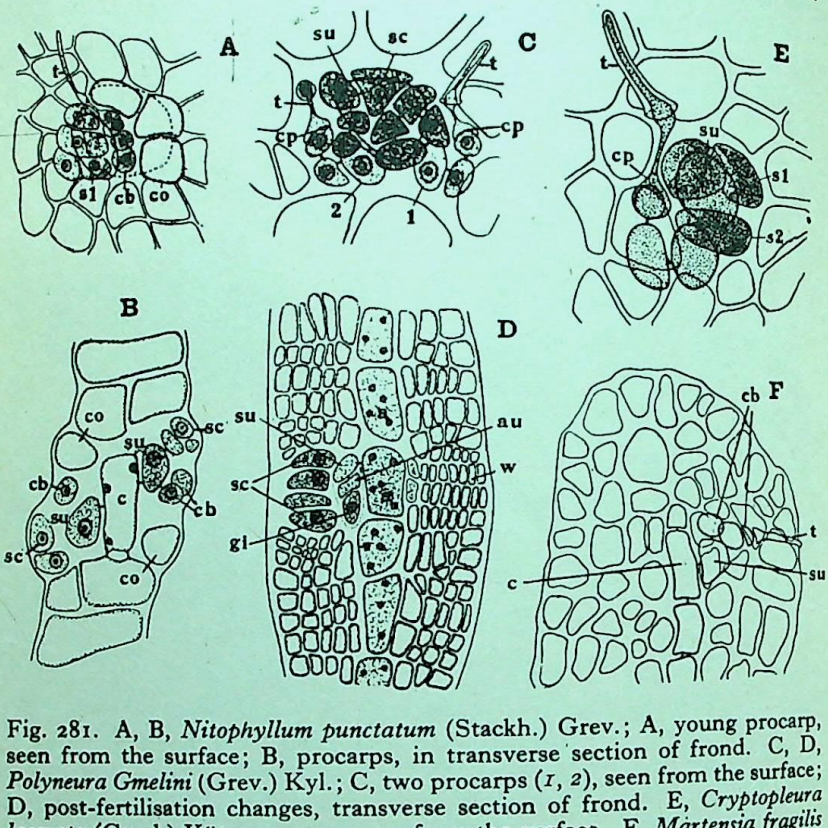

Fig. 281. A, B, *Nitophyllum punctatum* (Stackh.) Grev.; A, young procarp, seen from the surface; B, procarps, in transverse section of frond. C, D, *Polyneura Gmelini* (Grev.) Kyl.; C, two procarps (*1*, *2*), seen from the surface; D, post-fertilisation changes, transverse section of frond. E, *Cryptopleura lacerata* (Gmel.) Kütz., procarp seen from the surface. F, *Martensia fragilis* Harv., transverse section through fertile margin of lamella, with young procarp. *a*, axial cell; *au*, auxiliary cell; *c*, axial cell; *cb*, carpogonial branch; *co*, cortical cells; *cp*, carpogonium; *gi*, gonimoblast-initial; *s1*, *s2*, *sc*, sterile cells; *su*, supporting cell; *t*, trichogyne; *w*, wall of cystocarp. (F after Svedelius; the rest after Kylin.)

s1, *s2*) include very few cells. Diverse Nitophylleae form terminal carposporangia only. This is so in *Cryptopleura*, *Nitophyllum punctatum* (fig. 280 B; (382) p. 70, (396) p. 6), *Acrosorium* (509), and *Martensia*. *Nitophyllum* differs from other Delesseriaceae in that the fertile cell (fig. 281 B, *c*) cuts off on either surface two pericentrals, that first

[1] As *Nitophyllum*.

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formed (*co*) producing two or three ordinary cortical cells (fig. 281 A, *co*), while the other is the supporting cell (*su*), which, apart from the carpogonial branch (*cb*), bears only one group of sterile cells (*sc*).

In *Martensia* ((663) p. 81) the procarps arise within the margins of the longitudinal lamellae (p. 541). In a transverse section (fig. 281 F) the supporting cell (*su*) is seen to be cut off as usual from one of the axial cells (*c*), which are continuous with the single-layered part of the lamella. The cells of the carpogonial branch are multinucleate. The auxiliary cell is stated to establish connection with the second cell of the carpogonial branch, but this requires confirmation. The richly branched gonimoblast-threads are surrounded by a number of nutritive filaments, arising from the supporting and perhaps also from adjacent cells, but no fusion-cell is formed. The mature cystocarps appear as large swellings on the margins of the longitudinal lamellae.

The Delesseriaceae are almost invariably dioecious and the male plants are commonly smaller than the female or asexual ones, a feature which is very marked in *Caloglossa* and *Martensia*. In *Delesseria sanguinea* ((87) p. 296, (357) p. 255, (380) p. 103, (667)) the antheridial sori cover both surfaces (except for a narrow margin) of the minute male fronds. Those of *Membranoptera* ((87) p. 296, (380) p. 112) frequently occur on similar proliferations situated in the angles between the branches. In *Vanvoorstia* (508) they cover the ultimate blades, which have not yet anastomosed, while in *Gonimophyllum* ((27), (382) p. 95) they occupy practically the whole frond. The sori of *Martensia* (fig. 282 H, *a*; (663) pp. 59, 66) occur on either surface of the longitudinal lamellae.

In other Delesseriaceae the sori occupy more restricted areas. Thus, in *Apoglossum* ((87) p. 296, (357) p. 256, (380) p. 90), *Caloglossa Leprieurii* ((50) p. 343, (146) p. 9), and *Hypoglossum* ((85) p. 261) they are situated on either side of the midribs, while in *Phycodrys* ((357) p. 255, (380) p. 66) and *Cryptopleura* ((86) p. 249, (258) p. 198, (382) p. 88) they appear within the margins of the younger fronds (fig. 282 C); in the former they sometimes occupy special marginal proliferations. The marginal sori are often broken up into separate groups, as in *Polyneura* (fig. 282 F; (87) p. 295, (258) p. 194, (382) p. 43) and *Nitophyllum* ((382) p. 73, (475) p. 210). The minute male sori of *Grinnellia* ((75) p. 13) are irregularly scattered over the thallus (fig. 282 B).

The regions bearing antheridia always become several-layered (fig. 282 A, G), the many small mother-cells (*m*) being formed by anticlinal division of the pericentrals. As a general rule two or three antheridia are produced successively (fig. 282 D, E); in *Martensia* they are formed by abstriction (fig. 282 G) and occur in short rows.

(iii) *Rhodomelaceae.*

In most Rhodomelaceae (cf. (192) p. 108, (516), (517)) the procarps are formed on the trichoblasts (p. 544), generally on the suprabasal segment[1] (figs. 283 A, B; 284 A, *2*) which, like the basal segment (*1*),

[1] In *Rhodomela* ((192) p. 597, (558) p. 459) sometimes on the third or fourth segment.

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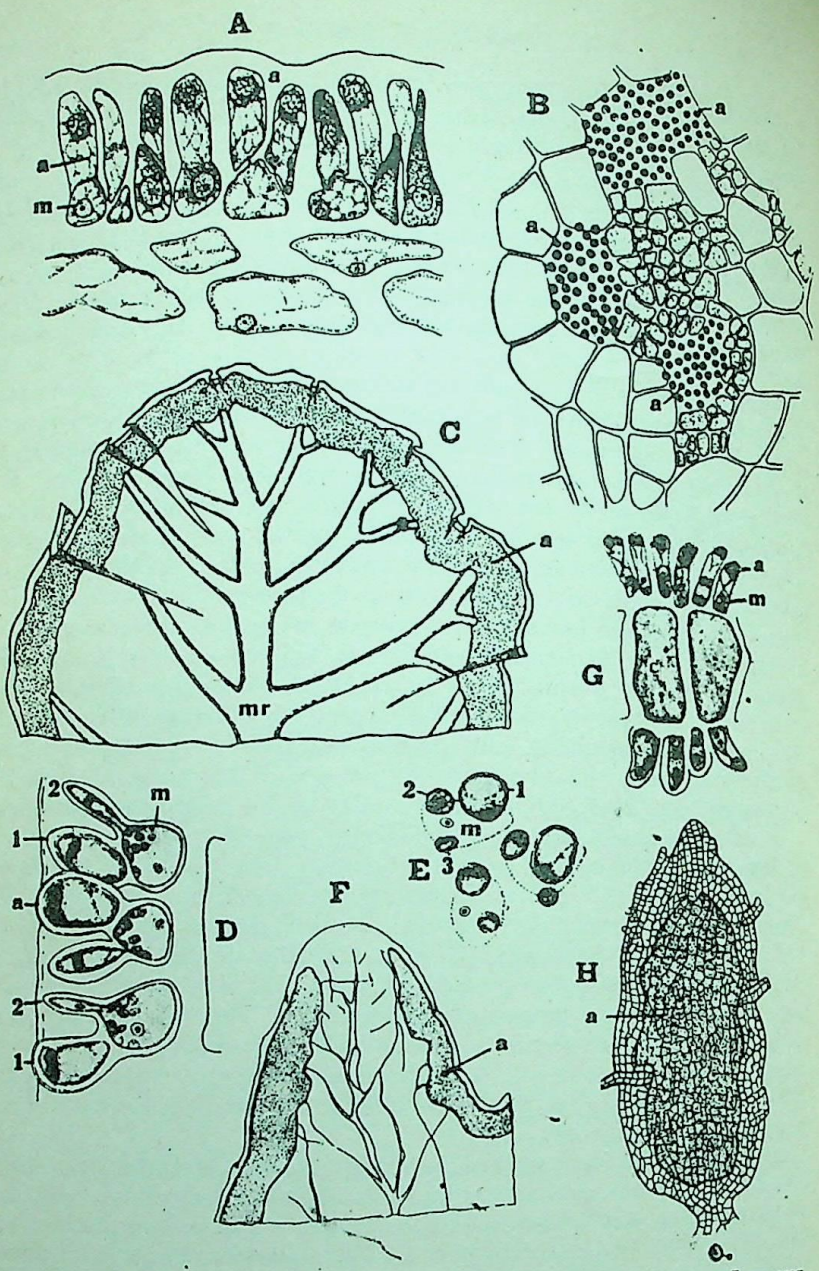

Fig. 282. Antheridia of Delesseriaceae. A, *Delesseria sanguinea* Lamour., transverse section of male frond, antheridium-development. B, *Grinnellia americana* (C. Ag.) Harv., development of antheridia seen from the surface. C, *Phycodrys rubens* (Huds.) Batt., part of frond with sori. D, E, *Polyneura Hilliae* (Grev.) Kyl., antheridium-formation; D, in section; E, in surface-view, the numerals indicate the order of development. F, *P. Gmelini* (Grev.) Kyl., part of frond with sori. G, H, *Martensia fragilis* Harv.; G, transverse section of part of lamella showing antheridium-development; H, surface-view of a lamella with sori. *a*, antheridia and antheridial sori; *c*, axial cell; *m*, antheridial mother-cells; *mr*, midrib. (A, G, H after Svedelius; D E after Grubb; the rest after Kylin.)

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becomes polysiphonous. The fertile segment normally produces five pericentrals (fig. 284 B–D). The first two (*1*, *2*) are cut off abaxially, the next two (*3*, *4*) on the flanks, and the fifth (*su*) on the adaxial (ventral) side; this last one gives rise to the procarp. It produces in succession (figs. 283 D; 284 A, *su*) a lateral sterile cell (*s1*), the four-celled carpogonial branch (*cb*), and lastly the second (basal) sterile cell (*s2*; cf. especially (397) p. 5), a sequence identical with that found in Delesseriaceae (p. 694). The first sterile cell, as in other Ceramiales, represents the only vegetative cell of the fertile lateral, while the second, which corresponds to that of Delesseriaceae and Dasyaceae, is homologous with a carpogonial branch (cf. also (516) p. 294, (605) pp. 232, 262). The sterile cells divide after fertilisation (fig. 283 F *sc*) and may fulfil a nutritive function ((389) p. 84), although it has also been suggested that they serve to separate the cystocarp-wall from the developing gonimoblast ((371) p. 45). The cells of the carpogonial branch are commonly binucleate (fig. 283 D; (756) p. 413). The auxiliary cell is cut off apically from the supporting cell, and the gonimoblast develops sympodially (cf. below). The cystocarps (figs. 283 J; 284 E; 285 D) always have a definite aperture and the wall is produced mainly from the two lateral pericentrals of the fertile trichoblast-segment (fig. 283 C, *e*). It is characteristic of Rhodomelaceae that this envelope usually commences to develop already prior to fertilisation.

These general features are well illustrated by *Polysiphonia*,[1] where the fertile trichoblasts arise just behind the apex. The development of the procarp (fig. 283 A–C) takes place as above described. The sterile cells, which Yamanouchi ((756) p. 416) incorrectly calls auxiliary cells, divide transversely after fertilisation (fig. 283 E, *sc*), while an open communication is established (fig. 283 I) between the carpogonium (*cp*) and auxiliary cell (*au*). In *P. decipiens* Connolly ((141) p. 131) describes the formation of a connecting cell, which fuses with the auxiliary cell; this has not been observed in other species, although recorded also in *Laurencia pinnatifida* ((380) p. 127). It is probable that only one of the two diploid nuclei (fig. 283 I, *dn*) passes into the auxiliary cell, which fuses with the supporting cell (*su*); later the fusion-cell also amalgamates with the axial cell of the fertile segment. The mode of development of the gonimoblast is peculiar to Rhodomelaceae ((192) p. 100). The initial gives rise to a number of short threads, the terminal cells of which develop into large and commonly pear-shaped carposporangia (fig. 283 J, *ca*), while the subterminal ones grow out into two-celled branches, the end-cells of which in their turn produce carpospores. This sympodial develop-

[1] See (141) p. 129, (380) p. 118, (397), (399), (516) p. 297, (547) p. 20, (710). The older literature ((67) p. 150, (68) p. 61, (586) p. 237, (590) p. 117) is only in part correct. Yamanouchi's account ((756) p. 418) of the events following on fertilisation do not agree in detail with those of any subsequent investigation.

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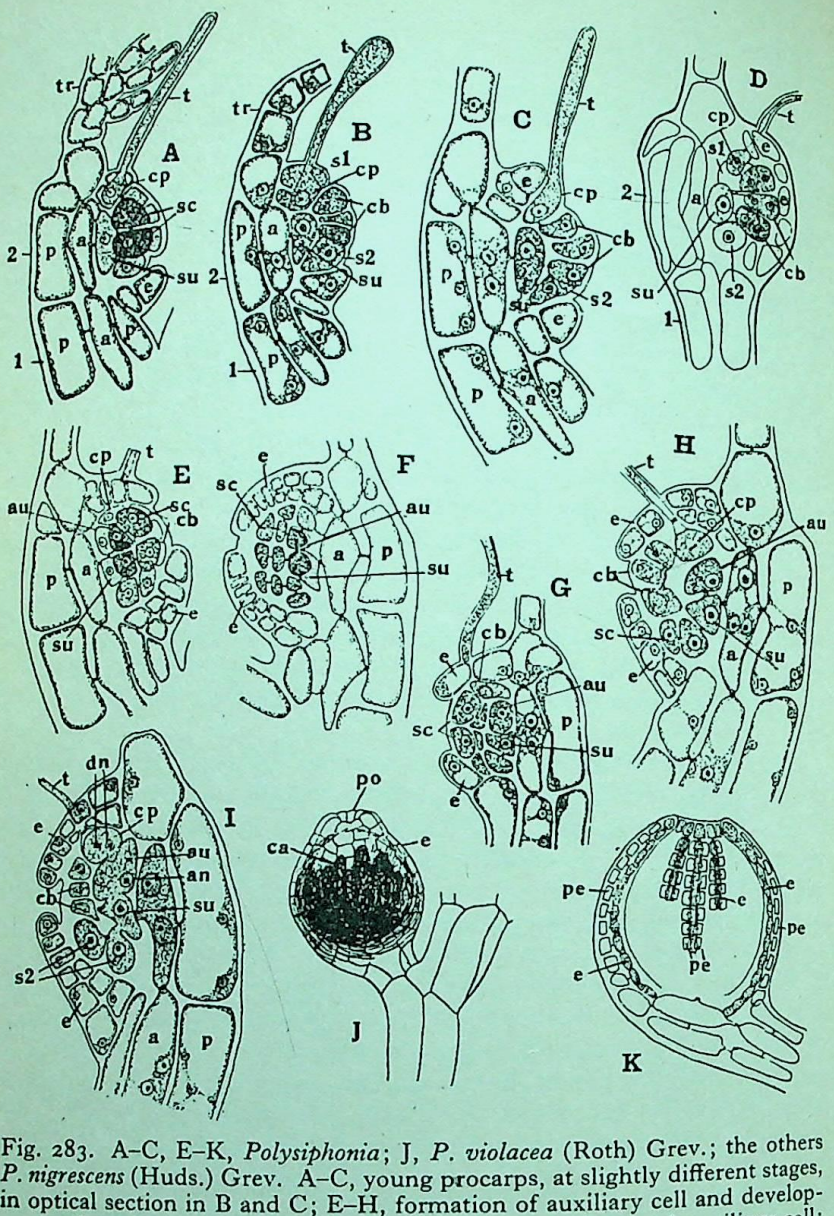

Fig. 283. A–C, E–K, *Polysiphonia*; J, *P. violacea* (Roth) Grev.; the others *P. nigrescens* (Huds.) Grev. A–C, young procarps, at slightly different stages, in optical section in B and C; E–H, formation of auxiliary cell and development of cystocarp-wall; I, fusion between carpogonium and auxiliary cell; J, mature cystocarp; K, structure of cystocarp-wall. D, *Brongniartella byssoides* (Good. & Wood.) Schmitz, procarp. *a*, axial cell; *an*, auxiliary cell nucleus; *au*, auxiliary cell; *ca*, carposporangia; *cb*, carpogonial branch; *cp*, carpogonium; *dn*, diploid nucleus; *e*, cystocarp-wall (in K inner layer of wall); *p*, pericentral; *pe*, outer layer of cystocarp-wall; *po*, aperture of cystocarp; *s1*, *s2*, *sc*, sterile cells; *su*, supporting cell; *t*, trichogyne; *tr*, trichoblast. The numerals *1*, *2* in A, B, D indicate the two basal segments of the trichoblast. (D after Rosenberg; J after Rosenvinge; K after Phillips; the rest after Kylin.)

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ment may continue for some time, the resulting threads bearing successively ripening carposporangia which are irregularly intermingled. Meanwhile the fusion-cell unites with the gonimoblast-initial and with the sterile cells ((141) p. 130, (389) p. 84, (521) p. 149).

The envelope of the cystocarp[1] originates, already before fertilisation (fig. 283 A, C–F, *e*), by the outgrowth of threads arising mainly from the lateral pericentrals of the fertile segment, although the adaxial pericentral of the basal segment (fig. 283 A, *1*) usually also plays a part ((192) p. 104, (380) p. 121). The young envelope (cf. especially fig. 283 C, D, *e*) consists of two lateral valves, composed of congenitally fused threads, which enclose the procarp like the shells of an oyster, the trichogyne (*t*) alone projecting. After fertilisation the two valves unite and each cell (fig. 283 K, *e*), except for the apical ones, cuts off two external pericentrals (*pe*); the envelope thus becomes two-layered, with twice as many rows of cells in the outer as in the inner layer. Bornet ((65) p. 306) describes an abnormal fruit, in which the threads composing the envelope were free at the apices and here formed pericentrals on all sides. The spherical or urn-shaped cystocarps (fig. 283 J) are borne on a short stalk, formed from the basal segment of the trichoblast, while the aperture (*po*) is directed upwards. The upper part of the trichoblast is usually shed. According to Rosenberg ((547) p. 24) *Brongniartella byssoides* shows altogether similar features.[2]

Other Rhodomelaceae differ in the main only in the position of the procarps and in the structure of the cystocarp-envelope. The fertile trichoblasts are, as in *Polysiphonia*, commonly branched (e.g. *Pollexfenia*; *Herposiphonia*, fig. 205 E, *t*; *Placophora*), but in *Rhodomela* ((192) p. 598, (371) p. 41, (380) p. 118, (516) p. 293) they are simple (fig. 284 A, *tr*).

Those of *Laurencia* ((380) p. 127) and *Chondria* ((192) p. 202, (387) p. 85, (397) p. 15, (517) p. 197)[3] consist of only three segments, the second (fertile) one being larger than the others (fig. 285 B, C). Developing procarps are found on trichoblasts still enclosed within the apical depression (p. 554) and fertilisation ensues before they have emerged from the latter. *Laurencia* is exceptional in producing only four pericentrals on the fertile segment. The urn-shaped cystocarps (fig. 285 A) are almost sessile (cf. also (50) p. 257). *Ricardia* ((54) p. 78, (387) p. 99, (397) p. 15) differs only in its embedded cystocarps. A similar reduction of the fertile trichoblasts is met with in diverse other specialised Rhodomelaceae (e.g. *Amansia* and *Vidalia*).

[1] Phillips' description of the development of the envelope was corrected by Falkenberg ((192) p. 106) and Connolly ((141) p. 135), as well as by himself ((521) p. 147). Yamanouchi ((756) p. 420), as well as Schussnig and Jahoda ((605) p. 236, for *Brongniartella*), however, erroneously follow the older account.

[2] The account of Schussnig and Jahoda ((605) p. 227) is erroneous in diverse respects (cf. (389) p. 80, (547) p. 26).

[3] The older descriptions relating to *Laurencia* ((192) p. 245, (517) p. 199) and *Chondria* ((326) p. 126, (692) p. 91) are not correct in all respects.

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Not all Rhodomelaceae, however, produce their procarps on definite trichoblasts. In *Odonthalia* ((192) p. 606, (397) p. 9) they are borne on cylindrical adventitious branches, arising from the margins of the fronds (fig. 284 E). The fertile segment is again mostly the second one and this produces five pericentrals in the usual sequence, so that it is probably justifiable to regard these branches as homologous with

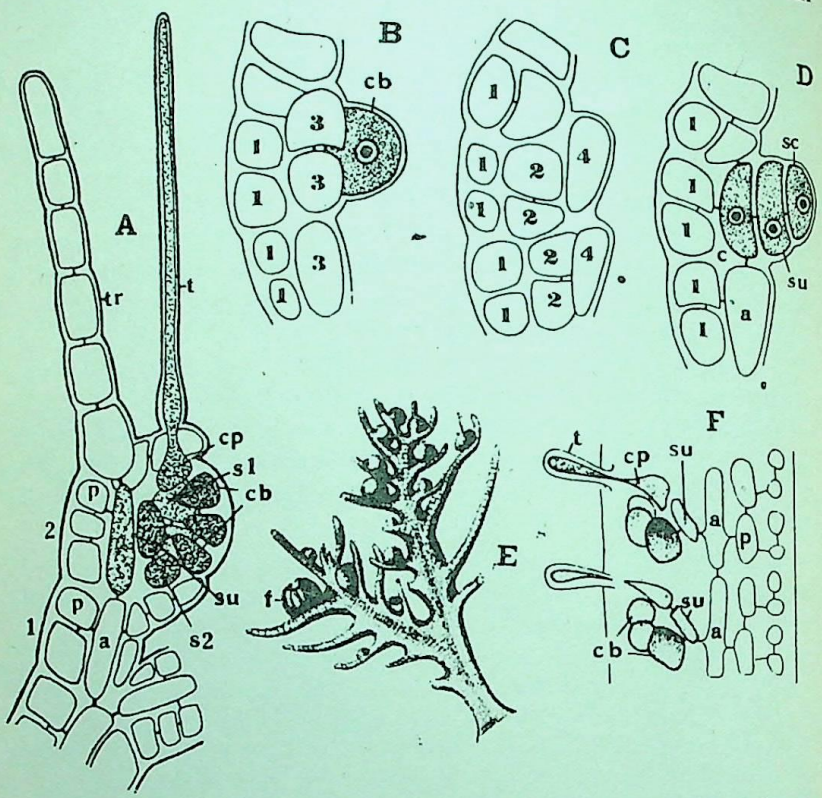

Fig. 284. A–D, *Rhodomela virgata* Kjellm.; A, young procarp; *1*, *2*, the two basal segments of the trichoblast; B–D, developing procarp, as seen (B) at a high, (C) at a low, and (D) at a median focus; the numerals indicate the successive pericentrals of each segment. E, *Odonthalia dentata* (L.) Lyngb., part of thallus with mature cystocarps (*f*). F, *Bostrychia scorpioides* (Gmel.) Mont., two procarps in a longitudinal section. *a*, *c*, axial cells; *cb*, carpogonial branch; *cp*, carpogonium; *p*, pericentral; *s1*, *s2*, *sc*, sterile cells; *su*, supporting cell; *t*, trichogyne; *tr*, trichoblast. (E, F after Falkenberg; the rest after Kylin.)

trichoblasts, although they do not show the usual hair-like character. The same interpretation should possibly be extended to the reduced fertile shoots of *Pterosiphonia* ((192) p. 262). The procarps (fig. 284 F) of *Bostrychia* ((192) p. 519) develop on several successive segments of the younger branches, although only one matures; the apex of the branch is pushed aside by the cystocarp so that the latter appears terminal.

In *Cliftonaea* and *Leveillea* the procarps are borne on laterals, consisting only of 3–4 segments ((192) pp. 378, 398) and arising from the

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lowest segment of a dwarf shoot (fig. 285 E, *fb*); in the former the upper part of this shoot produces branched trichoblasts. According to Falkenberg the fertile laterals arise endogenously and are not of the nature of trichoblasts, a matter meriting further enquiry.

In certain genera (*Rhodomela*, *Laurencia*, *Chondria*) the envelope of the mature cystocarp is composed of more than two layers owing to tangential division of the pericentrals. *Bostrychia* is exceptional in that the envelope develops only after fertilisation.

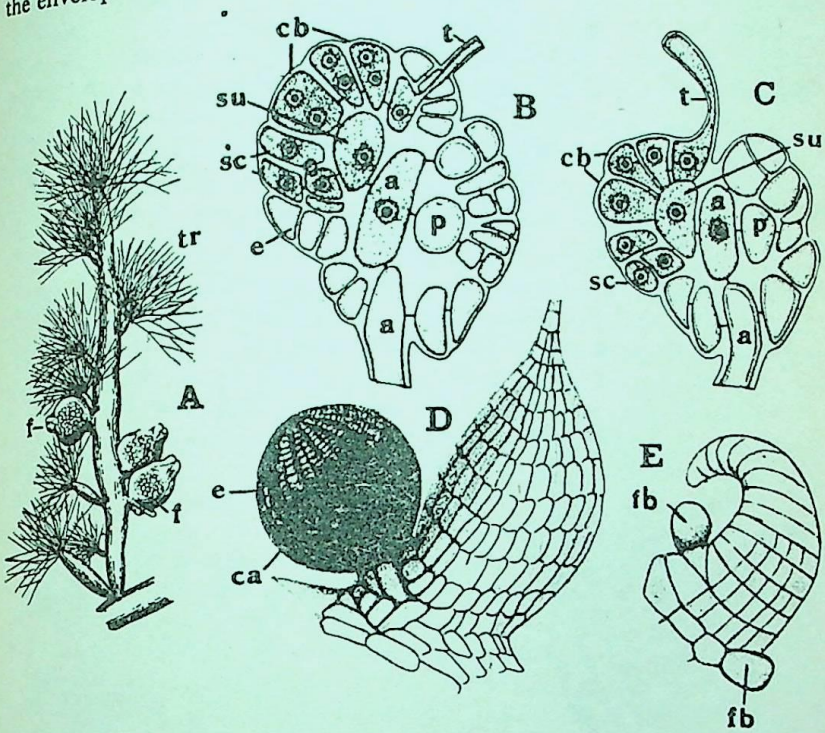

Fig. 285. A, *Chondria tenuissima* (Good. & Wood.) C. Ag., branch bearing cystocarps (*f*). B, C, *C. dasyphylla* (Woodw.) C. Ag., two procarps. D, E, *Leveillea jungermannioides* (Mart. & Her.) Harv.; D, shoot of limited growth, with almost ripe cystocarp; E, the same, with young fertile branches (*fb*). *a*, axial cell; *ca*, carposporangia; *cb*, carpogonial branch; *e*, cystocarp-wall; *p*, pericentral; *sc*, sterile cells; *su*, supporting cell; *t*, trichogyne; *tr*, trichoblasts. (A after Taylor; B, C after Kylin; D, E after Falkenberg.)

The vast majority of Rhodomelaceae are dioecious ((347) p. 244), the males sometimes smaller than the females (*Brongniartella* ((605) p. 222)); in *Janczewskia* male and female plants have a different habit. The antheridial sori are again commonly borne on the branches of typical trichoblasts, although in several of the more specialised genera (*Symphyocladia*, *Herposiphonia*, *Placophora*, *Amansia*) the sterile part of the trichoblast is greatly reduced. In *Polysiphonia* ((84) p. 343, (85) p. 263, (258) p. 208, (380) p. 121, (558) p. 409 et seq., (692) p. 85, (710)) the male trichoblasts (fig. 286 B) commonly consist of a two-celled stalk

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(*st*) surmounted by the fertile region (*f*); the upper stalk-cell frequently bears a branch (*t*), the upper part of which may again be fertile. The fertile regions (fig. 286 A, *f*) become polysiphonous and

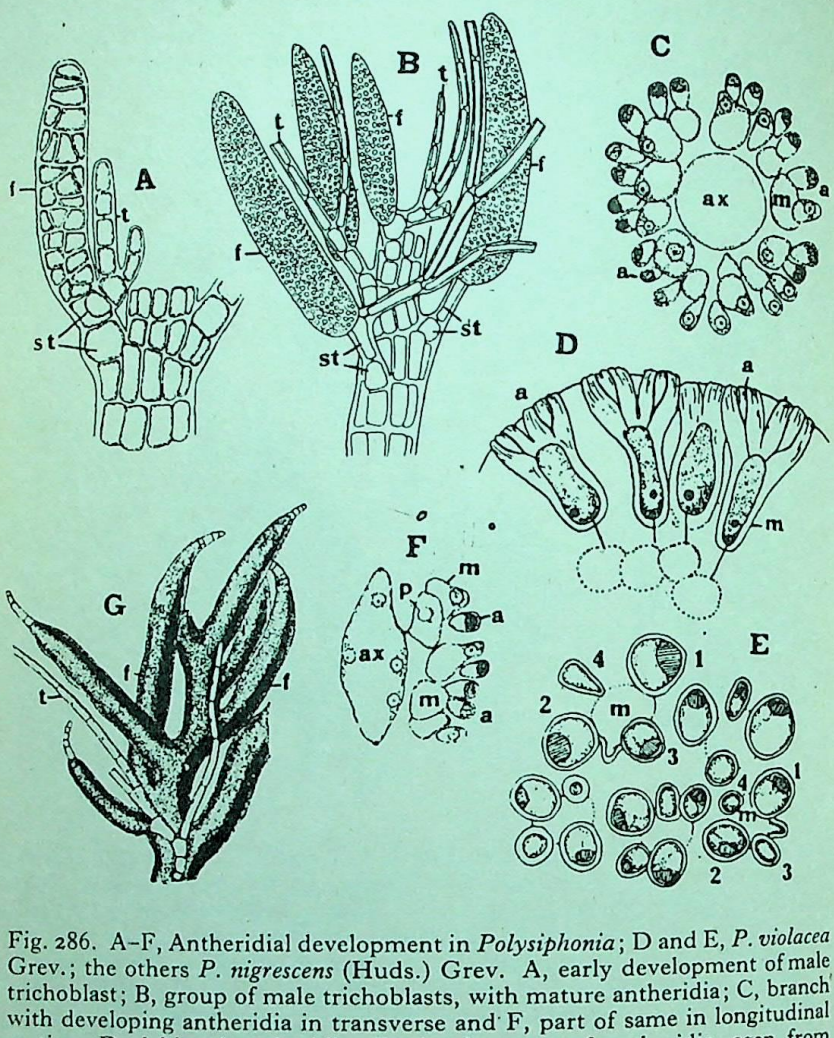

Fig. 286. A–F, Antheridial development in *Polysiphonia*; D and E, *P. violacea* Grev.; the others *P. nigrescens* (Huds.) Grev. A, early development of male trichoblast; B, group of male trichoblasts, with mature antheridia; C, branch with developing antheridia in transverse and F, part of same in longitudinal section; D, dehisced antheridia; E, development of antheridia, seen from the surface, the numerals indicating the succession. G, *Rhodomela subfusca* (Woodw.) Ag., male branches. *a*, antheridium; *ax*, axial cell; *f*, fertile branch of trichoblast; *m*, antheridial mother-cell; *p*, pericentral; *st*, sterile basal cells of antheridial branch; *t*, sterile branch of trichoblast. (D, E after Grubb; the rest after Kylin.)

the pericentrals divide copiously (fig. 286 C, F) to form a compact layer of mother-cells (*m*), each of which gives rise to 2–3 antheridia (occasionally 4–5, fig. 286 E). *Brongniartella* ((605) p. 239) and *Ricardia* ((54) p. 78, (387) p. 101) are similar.

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In *Laurencia* ((87) p. 298, (192) p. 247, (258) p. 201, (380) p. 129, (690) p. 17) the fertile tips of male plants become swollen, since the apical cell ceases to divide and the apical depression becomes markedly broadened (fig. 287 A). The resulting cup- or urn-shaped cavities contain numerous fertile trichoblasts (*t*), which are interspersed with sterile ones in *L. obtusa*. In *L. pinnatifida* (fig. 287 C–E) the segments of the trichoblasts form a continuous layer of mother-cells (*m*), as in *Polysiphonia*, each producing (fig. 287 K) three or four primary, as well as secondary (*sa*), antheridia. The fertile trichoblasts of *L. obtusa*, on the other hand, remain uniseriate (fig. 287 J), but bear branches on which the mother-cells (*m*) are formed. According to Grubb ((258) p. 205) mother-cells can also arise from the cells lining the cavities. Each male trichoblast (fig. 287 B) terminates in one or more, often huge, sterile cells (*v*), which collapse at a later stage.

The antheridial sori of *Chondria* ((85) p. 262, (192) p. 201, (259) p. 179, (690) p. 17, (692) p. 90) occupy the lowest lateral of a trichoblast. The branchlets of the fertile lateral (fig. 287 G) remain concrescent from the first and form a biconvex disc, the edge of which is occupied by the enlarged and sterile apical cells (*st*) of the individual branchlets (cf. also fig. 287 F). The remaining cells cut off, on either surface, pericentrals (*p*) which produce a continuous layer of globular mother-cells (*m*), each forming three or four cylindrical antheridia (*a*). Similar discs with concrescent branches occur in *Acanthophora* ((21) p. 48), *Pterochondria* ((781) p. 532) and *Bryothamnion* ((192) p. 175), as well as in *Cliftonaea* ((192) p. 380) and *Leveillea* (fig. 287 H, I; (192) p. 399), although in the last two they appear to represent modified shoots and develop rather differently.

In *Odonthalia* ((87) p. 297, (192) p. 607, (307) p. 8) and *Rhodomela* ((371) p. 55, (557) p. 463) the antheridia are mostly formed on fertile polysiphonous laterals, simple in the former, often branched in the latter (fig. 286 G), although in *R. subfusca* they can also arise on trichoblasts ((85) p. 262, (558) p. 456). There is little reason to doubt that the male branches of these two genera, however different they may be from the normal type, are homologous with the trichoblasts.

(iv) *Dasyaceae.*

As in vegetative construction, so also in their sexual reproduction, the Dasyaceae exhibit distinct differences from Rhodomelaceae. The procarps are formed either on the sympodial axis (*Dasya pedicellata*, *Dasyopsis*) or on a pseudolateral (*Dasya arbuscula* (548) p. 537; *Heterosiphonia*). The fertile pericentral of the procarp-bearing segment is usually the third (sometimes the fourth) and only in *Heterosiphonia* is it the fifth or last-formed one. The procarp develops as in Rhodomelaceae (fig. 288 A), but the cystocarp-envelope appears only after fertilisation. The gonimoblast shows monopodial branching (fig. 288 D).

In most species of *Dasya* ((192) p. 620, (499) p. 119, (516), (547) p. 39) and in *Dasyopsis* ((547) p. 55) the procarps arise from successive seg-

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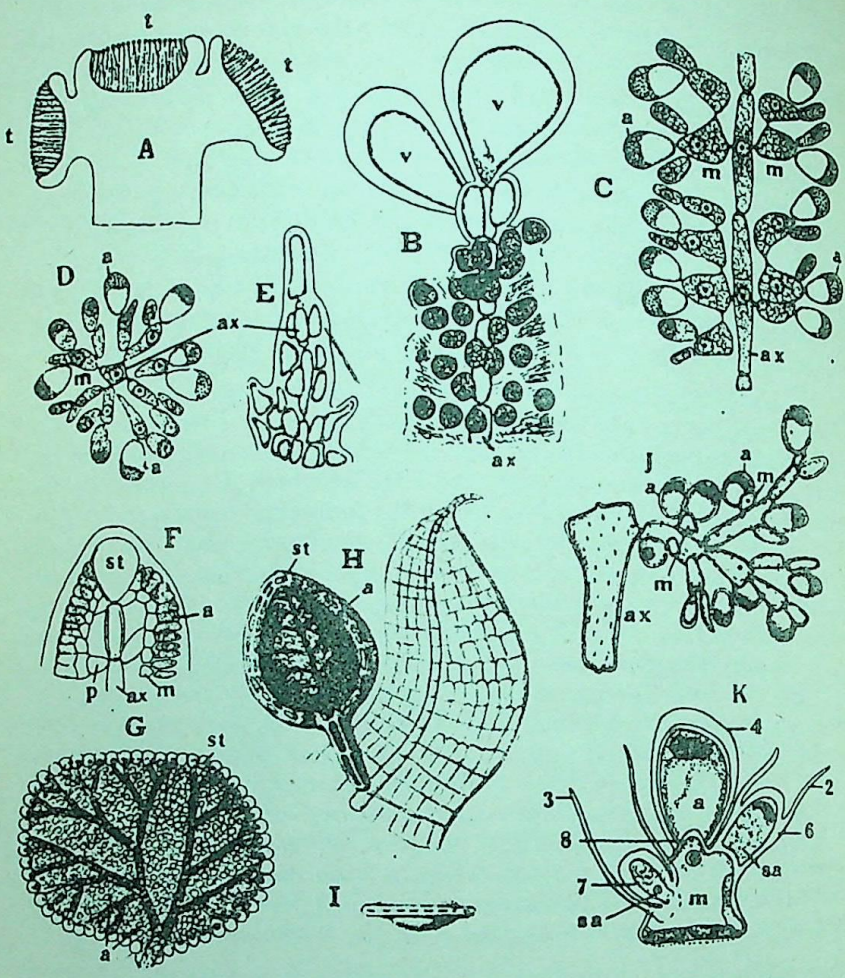

Fig. 287. Antheridia of Rhodomelaceae. **A–E,** *Laurencia pinnatifida* (Gmel.) Lamour.; A, longitudinal section of apex with three antheridial depressions; B, apex of a male trichoblast; C, the same, in longitudinal and D, in transverse section, antheridial development; E, apex of young male trichoblast. F, G, *Chondria dasyphylla* (Woodw.) C. Ag.; F, tip of male branch, in vertical section; G, the same, seen from the surface. H, I, *Leveillea jungermannioides* (Mart. & Her.) Harv.; H, shoot of limited growth, with a male branch; I, transverse section of same. J, K, *Laurencia obtusa* (Huds.) Lamour. J, small part of a male trichoblast; K, sequence of antheridial development (*2–8*). *a*, antheridium; *ax*, axial cell; *m*, antheridial mother-cell; *p*, pericentral; *sa*, secondary antheridium; *st*, sterile borders of antheridial branches; *t*, trichoblasts; *v*, vesicular cells. (A–E after Kylin; F–I after Falkenberg; J, K after Grubb.)

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ments of the sympodial axes or more usually (*D. pedicellata*, *Dasyopsis plumosa*) of adventitious branches (fig. 288 A); as a general rule only one cystocarp matures on each branch. One (or possibly two) small

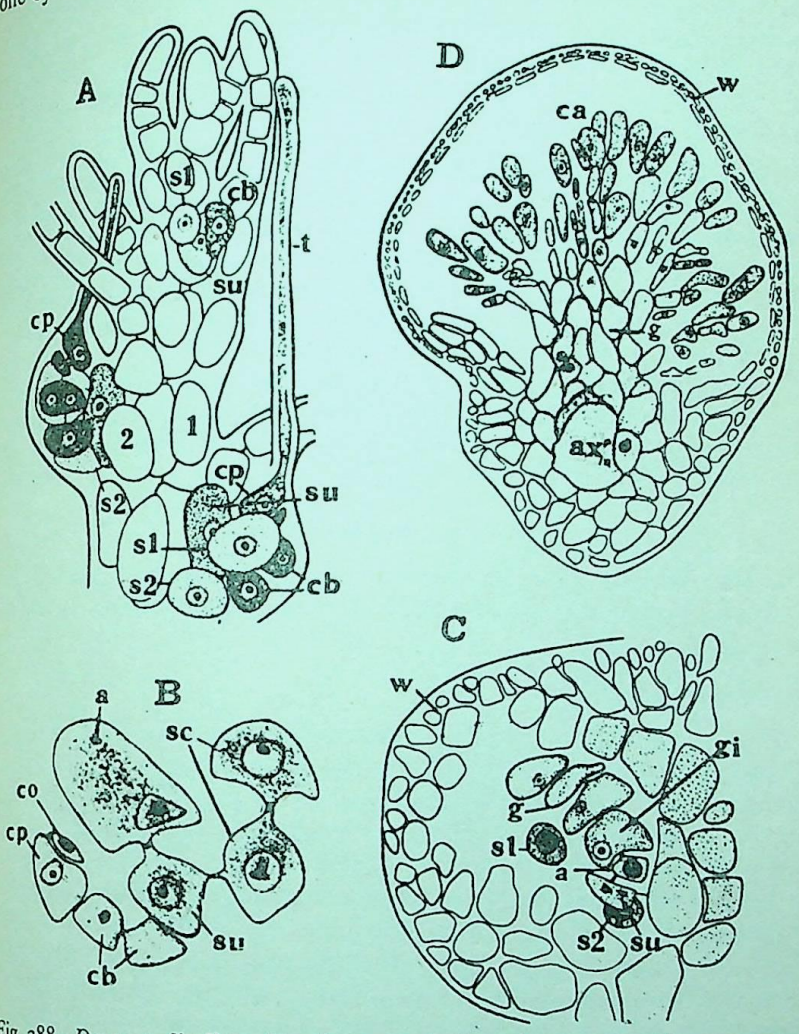

Fig. 288. *Dasya pedicellata* Ag. A, apex of a branch-system, with young procarps; B, formation of auxiliary and connecting cells; C, early development of gonimoblast and cystocarp-wall; D, young cystocarp in transverse section. *a*, auxiliary cell; *ax*, axial cell; *ca*, carposporangia; *cb*, carpogonial branch; *co*, connecting cell; *cp*, carpogonium; *g*, gonimoblast; *gi*, gonimoblast-initial; *s1*, *s2*, *sc*, sterile cells; *su*, supporting cell; *t*, trichogyne; *w*, wall of cystocarp; *1*, *2* (in A), pericentrals. (B after Oltmanns; the rest after Rosenberg.)

connecting cells (fig. 288 B, *co*) are cut off from the fertilised carpogonium (*cp*) and fuse with the auxiliary cell (*a*). The gonimoblast-initial (fig. 288 C, *gi*) first forms a row of large cells (*g*), which cut off smaller ones giving rise to branched threads (fig. 288 D, *g*) that fill

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the cavity of the cystocarp; the carposporangia (*ca*) form short rows arising in basipetal sequence. According to Rosenberg ((547) p. 46) no fusion-cell is formed (cf. however (192) p. 621). The cystocarps (fig. 214 A, *cy*) are provided with a pore. The envelope, which originates from the two pericentrals flanking the fertile one, as well as from pericentrals of adjacent segments, is formed in the same way as in *Polysiphonia* and is two-layered (three-layered in *Dasyopsis*) at maturity.

The procarps of *Heterosiphonia plumosa*[1] ((326) p. 129, (442) p. 390, (517) p. 187, (547) p. 65) usually arise from the fourth segment of the pseudolateral and possess very elongate trichogynes; the sterile cells here undergo considerable division before fertilisation. The pericarp develops already during the formation of the carpogonial branch and is three-layered at maturity. The cystocarps of *Dictyurus* are unknown; regarding those of *Thuretia*, see (192) p. 672.

The antheridia ((5) p. 78, (85) p. 263, (547) pp. 48, 73, (548) p. 540, (558) p. 403) are produced on the pseudolaterals, although in *Dasya pedicellata* they may also arise on adventitious branches. The development of the sori takes place as in *Polysiphonia*.

(*b*) *The Asexual Phase*

The four families differ markedly in the mode of production of the tetrasporangia, and it is again the Ceramiaceae that exhibit relatively primitive features.

(i) *Ceramiaceae*.

The tetrasporangia of most Ceramiaceae stand quite freely, though occupying diverse positions. In *Antithamnion* and related genera they commonly occur in series on the upper sides of the laterals (figs. 185 A; 289 B, *t*), being either sessile or situated at the ends of one- or two-celled branchlets ((558) p. 315 et seq., (692) p. 71, (733) p. 133, (736) p. 198). Sometimes, however, they are clustered together on short branches, as in *A. cruciatum* (fig. 289 A), *Spermothamnion* and *Compsothamnion* ((737) p. 359). In *Crouania* ((50) p. 232) they are borne on the basal cells of the whorled laterals, while in *Ptilota plumosa* ((380) p. 59, (558) p. 357) the sporangia for the most part occupy short threads arising from the cortex of the ultimate branches.

The sporangia of *Griffithsia* ((50) p. 205, (375) p. 116, (428) p. 663, (751) p. 507) are produced on special laterals (fig. 289 D, *f*) which form whorls at the apices of the segments. Each fertile lateral (fig. 289 E) consists of a single cell (*s*), bearing several sporangia (*t*) and protected by outgrowths (*e*), arising from the same cell or from the parent-segment. Similar protective branches are seen in *Wrangelia* ((50) p. 121, (386) p. 7, (766) p. 379), where the sporangia are terminal on one-celled accessory branchlets (fig. 289 I, J) arising from the lower cells

[1] Cf. also (21) p. 52 regarding *H. Berkleyi* (*Dasya Berkleyi* (Mont.) J. Ag.).

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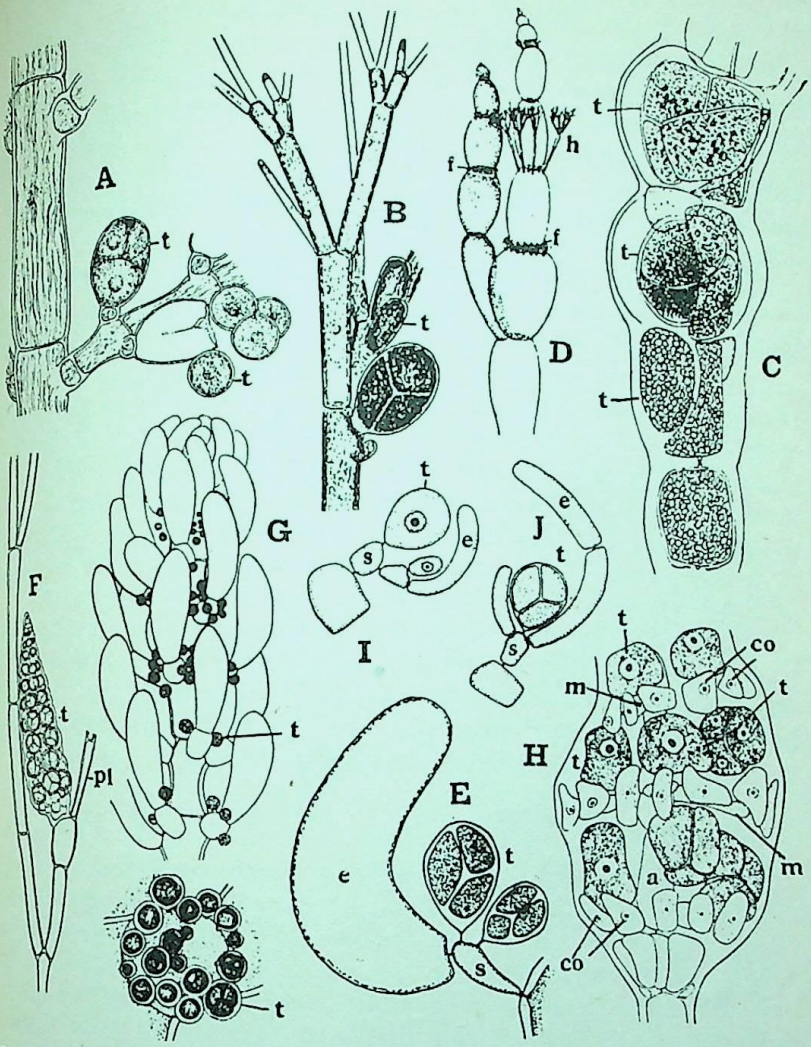

Fig. 289. Tetraspore-formation in Ceramiaceae and Dasyaceae. A, *Antithamnion cruciatum* (Ag.) Naeg. B, *Callithamnion corymbosum* (Engl. Bot.) Ag. C, *Trailiella intricata* (J. Ag.) Batt. D, *Griffithsia globifera* (Harv.) J. Ag., apex of a tetraspore-bearing plant. E, *G. pacifica* Kyl., single fertile branch. F, H, *Dasya pedicellata* Ag.; F, stichidium; H, details of sporangial development. G, *Vickersia baccata* (J. Ag.) Karsak., branch producing sporangia; below, the basal cell with a sporangial sorus. I, J, *Wrangelia penicillata* C. Ag., fertile branches. *a*, axial cell; *co*, cover-cells; *e*, enveloping threads; *f*, fertile threads; *h*, hairs; *m*, mother-cell of sporangium; *pl*, pseudolateral; *s*, stalk-cell; *t*, tetrasporangium. (A, F after Taylor; B after Thuret & Bornet; C after Rosenvinge; D after Lewis; E, I, J after Kylin; G after Boergesen; H after Rosenberg.)

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of the whorled laterals. In *Vickersia* ((54) p. 24) the sporangia form sori on short cells cut off at the base of the vesicular laterals (fig. 289 G).

In *Ceramium*, on the other hand, the sporangia are enlarged cells of the cortical bands (fig. 187 B, *t*), within which they are partly embedded. Those of *Spyridia* occur on the "filaments" (fig. 188 A, B). A peculiar method of development, in some respects recalling that of Rhodomelaceae, is met with in *Trailiella* ((30) p. 10, (558) p. 306), where the sporangia are formed from the larger halves of longitudinally divided cells of the erect filaments (fig. 289 C).

The spores are for the most part tetrahedrally arranged (fig. 289 B, E), although those of *Crouania*, *Antithamnion* (fig. 289 A), and *Trailiella* (fig. 289 C) are cruciate. *Antithamnionella* ((437), (462) p. 378, (712) p. 5) differs essentially from *Antithamnion* only in possessing tetrahedral spores. There is, however, some variability in this respect (706); thus, in *Ceramium* ((558) p. 373) and *Seirospora* ((590) p. 116) cruciate and tetrahedral sporangia are sometimes found on the same plant, although in both cleavage only takes place after nuclear division is completed. In *Callithamnion byssoides* Boergesen ((46) p. 13, (50) p. 219) also records occasional cruciate tetrasporangia. The sporangia of *Callithamnion* dehisce by the detachment of a lid (fig. 294 K).

Bispores are recorded in diverse Ceramiaceae ((478) p. 384, (736) p. 199) and are specially frequent in *Crouania attenuata* and *Callithamnion Furcellarieae* ((558) pp. 341, 350); in the latter they occur on plants lacking tetrasporangia (fig. 294 L). In *C. bisporum* Gardner (237) they are the only reproductive organs known.[1]

(ii) *Delesseriaceae.*

The sporangia of Delesseriaceae, in which the spores are always tetrahedrally arranged (fig. 290 D, L), generally show a distribution comparable to that of the sex organs. In *Delesseria sanguinea* ((380) p. 105, (665) p. 272) they are formed in minute leaflets, which are devoid of a midrib and soon become three-layered almost throughout. Subsequently the surface-cells divide to form short vertical branch-systems (fig. 290 D, *c*), from the terminal cells of which the sporangia (*t*) develop. Though primarily superficial, as in all Delesserieae, the initials (*t*) gradually become covered by small cells (*co*), produced by further division of the surrounding elements. The enlargement of the sporangia causes gaps to be formed between these cells, through which the spores are shed.

Development follows much the same course in other Delesserieae (fig. 290 F), although the position of the sporangia varies. In *Membranoptera* ((380) p. 112) they are situated in the younger forks or in small proliferations, in *Grinnellia* ((382) p. 23) in small scattered out-

[1] A further consideration of these bispores, as well as of other special asexual reproductive cells of Ceramiaceae, will be found on p. 728 *et seq.*

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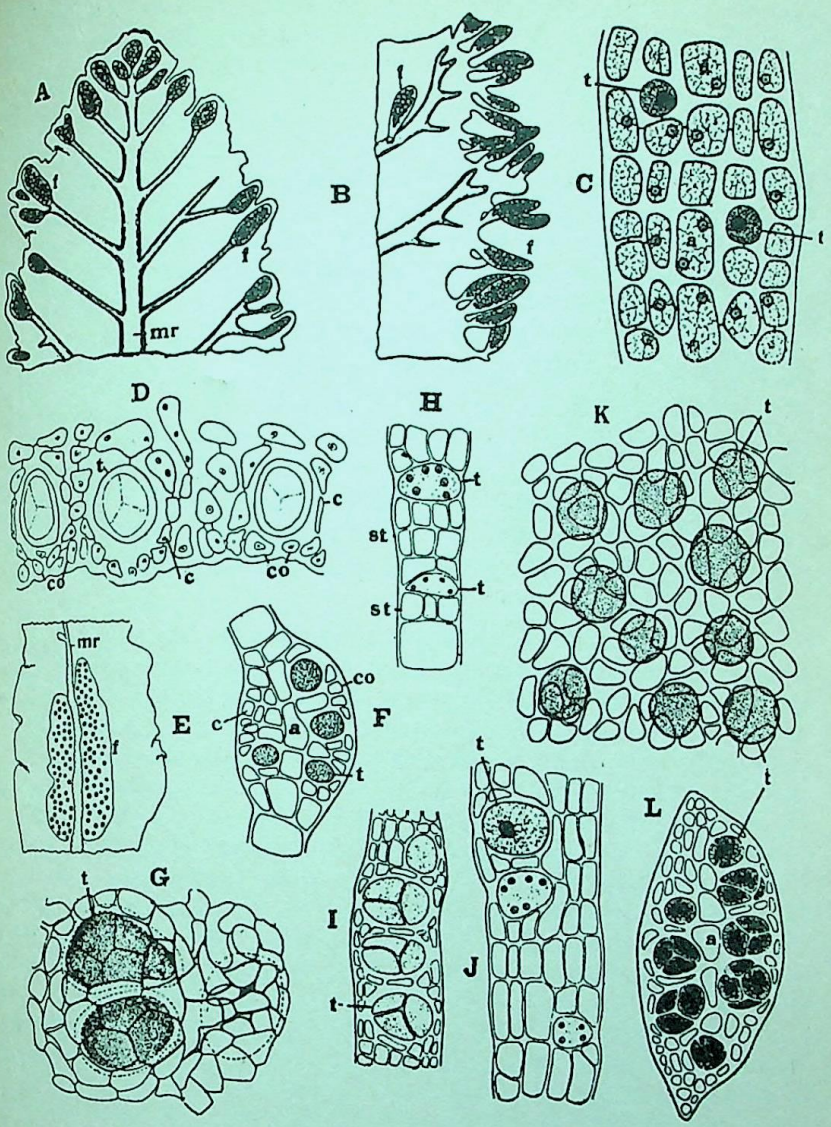

Fig. 290. Tetraspore-formation in Delesseriaceae. A–C, K, L, *Phycodrys rubens* (Huds.) Batt.; A, B, parts of two fertile fronds; C, vertical section of thallus, with sporangial rudiments; K, young sporangia in surface-view; L, transverse section of fertile zone, with ripe sporangia. D, *Delesseria sanguinea* Lamour., part of vertical section of thallus, with ripe sporangia. E, *Hypoglossum Woodwardii* Kütz., part of a fertile blade. F, *Grinnellia americana* (C. Ag.) Harv., vertical section of young fertile frond. G, *Martensia fragilis* Harv., two young sporangia in surface-view. H–J, *Nitophyllum punctatum* (Stackh.) Grev., vertical sections of fertile fronds; H, with multinucleate and J, with one mature initial; I, ripe sporangia. *a*, axial cell *c*, cortex; *co*, cover-cells; *f*, fertile zone; *mr*, midrib; *st*, sterile zone; *t*, tetrasporangium. (D, G after Svedelius; the rest after Kylin.)

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growths (fig. 190 A, *t*), commonly confined to one surface, while in *Hypoglossum* (fig. 290 E; (382) p. 9), *Caloglossa* ((146) p. 6, (380) p. 108), and *Apoglossum* ((380) p. 91) they occupy elongate areas on either side of the midrib of the ordinary fronds. In *Caloglossa* they develop by the division of certain cells in parts of the frond that are still monostromatic so that the sporangia form but a single layer, instead of two, as in other Delesserieae (cf. fig. 290 F); they are subsequently covered by a cortex formed by pericentrals cut off tangentially from the parent-cells. The sporangia of *Claudea* and *Vanvoorstia* (508) are formed from pericentrals (in *Claudea* also from the cortical threads) in the ultimate blades, before they undergo anastomosis.

The sporangia of *Phycodrys rubens* ((380) p. 65) are usually borne in small marginal proliferations (fig. 290 B, *f*), but they sometimes occupy oblong areas at the ends of the veins of the younger fronds (fig. 290 A, *f*). The fertile tracts (fig. 290 C) soon become five-layered. The sporangial initials (*t*) are, as in all Nitophylleae, cut off from internal cells, in *Phycodrys* from the hypodermal ones. This is also so in *Acrosorium* ((509) p. 20), *Polyneura* ((382) pp. 37, 43), and *Cryptopleura* ((382) p. 88) where, however, sporangia may also arise from the central cells.

The sporangial sori of *Polyneura*, *Cryptopleura*, and *Nitophyllum* are small and irregularly scattered. In *N. punctatum* ((382) p. 74, (669) p. 49) the sporangia may occupy the whole thickness of the frond (fig. 290 H, *t*), although sometimes embedded (fig. 290 J). Their formation is initiated by intercalary division of groups of cells in the one-layered thallus; some of the resulting elements develop into sporangia (fig. 290 H, *t*), while the remainder (*st*) cut off pericentrals, from which further sporangia may arise (fig. 290 J, *t*). The sporangia of *Nitophyllum* thus show pit-connections with several surrounding cells, whereas in other Delesseriaceae they are only connected with their mother-cell (fig. 290 C, D). Those of *Martensia* ((663) p. 46) occur within swollen areas on the longitudinal lamellae (fig. 290 G), more rarely on the entire portion of the thallus. Both here and in *Nitophyllum punctatum* (figs. 290 H; 293 A) the initials are multinucleate but, although several nuclei may show the first stages of meiosis, only one survives (figs. 290 J; 293 B) to form the tetraspore-nuclei.

(iii) *Rhodomelaceae.*

The sporangia of Rhodomelaceae nearly always possess tetrahedrally arranged spores (fig. 291 D, G, L) and are usually immersed in polysiphonous branches. They are only rarely borne on trichoblasts, as in *Lophocladia* (fig. 291 L) and *Wrightiella* (fig. 299 H). The fertile branches are often specially differentiated, constituting so-called *stichidia*, although the term cannot be exactly defined ((192) p. 86). The initials are usually (except *Laurencia*) formed from pericentral cells (fig. 198 G, *te*) and, as a general rule, one sporangium is produced in each segment (fig. 291 D, L); development often follows

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a regular basipetal sequence within the fertile branch. If the latter is unbranched, the sporangia of successive segments are generally superposed; when laterals (commonly trichoblasts) are present, the sporangia show a spiral arrangement like that of the laterals.

The segments of the stichidia often possess five pericentrals, whatever be the number in the vegetative branches. The fertile pericentral, which is seemingly never the first-formed one[1] ((547) p. 32, (549) p. 10, (558) p. 465; cf. however (192) p. 88, (605) p. 240), cuts off two superficial cover-cells (fig. 291 A, B, I, *co*), after which the sporangial initial (*t*) is produced on the apical side; the small bearing cell (*m*) is linked by primary pit-connections with the axial (*a*) and covering cells (*co*) (cf. also fig. 198 G and (380) p. 123, (399) p. 4). The similarity in position of sporangium and bearing cell on the one hand, and of auxiliary and auxiliary mother-cells on the other hand, is noteworthy ((192) p. 99); the cover-cells correspond to the sterile cells and carpogonial branch of a procarp. The mature spores escape between the cover-cells which are more or less displaced. In *Falkenbergia* ((192) p. 691, (495)) the sporangia arise from an entire pericentral and there are no cover-cells.

In *Polysiphonia* (fig. 291 D) the sporangia often cause irregular swellings within the stichidia (cf. also fig. 291 L). The fertile branches of *Rhodomela* ((371) p. 59, (558) p. 457) and *Odonthalia* ((397) p. 8) arise in tufts on the flanks, in the former also on the tips of the larger branches. The sporangia (fig. 291 G, I) originate from the two lateral of the six pericentrals (fig. 291 C, *t*) so that they form two longitudinal rows. *Bostrychia* ((50) p. 301, (192) pp. 88, 504) produces its sporangia in the ultimate branches (fig. 291 H), in which all the pericentrals of a segment commonly become fertile, although in certain species those on the dorsal side remain sterile. Similar dorsiventral stichidia occur in *Colacopsis* (fig. 299 F, G).

The sporangia of *Chondria* ((387) p. 89) develop within the apical depression of club-shaped branchlets, the initial here producing three cover-cells. Those of *Laurencia* ((192) p. 244, (380) p. 130, (387) p. 94) likewise originate within the apical pit, but are exceptional in being produced from young cortical cells; this is also so in *Ricardia* ((54) p. 78, (387) p. 101). In *Acanthophora* the sporangia occupy the spiny laterals.

Many of the more specialised Rhodomelaceae (e.g. *Herposiphonia*, fig. 291 K) possess stichidia resembling those of *Polysiphonia*. In *Pollexfenia* ((192) p. 294) these free polysiphonous, and often branched, laterals either occupy the growing margin (*P. crispata*) or arise on the surface of the flat thallus (*P. pedicellata*, fig. 207 G, *f*). *Placophora* ((192) p. 341, (247) p. 4) shows much the same (fig. 208 A, *r*; F). In other instances, however, the fertile shoots show a more profound modification. Thus, in *Cliftonaea* ((192) p. 381) each segment of a fertile long shoot

[1] According to Rosenberg (547) it is generally the second in *Polysiphonia nigrescens* and *Brongniartella byssoides*, the third in *Polysiphonia Brodiaei* and *P. violacea*. Harvey-Gibson's (280) account of sporangium-formation in *Polysiphonia* is incorrect.

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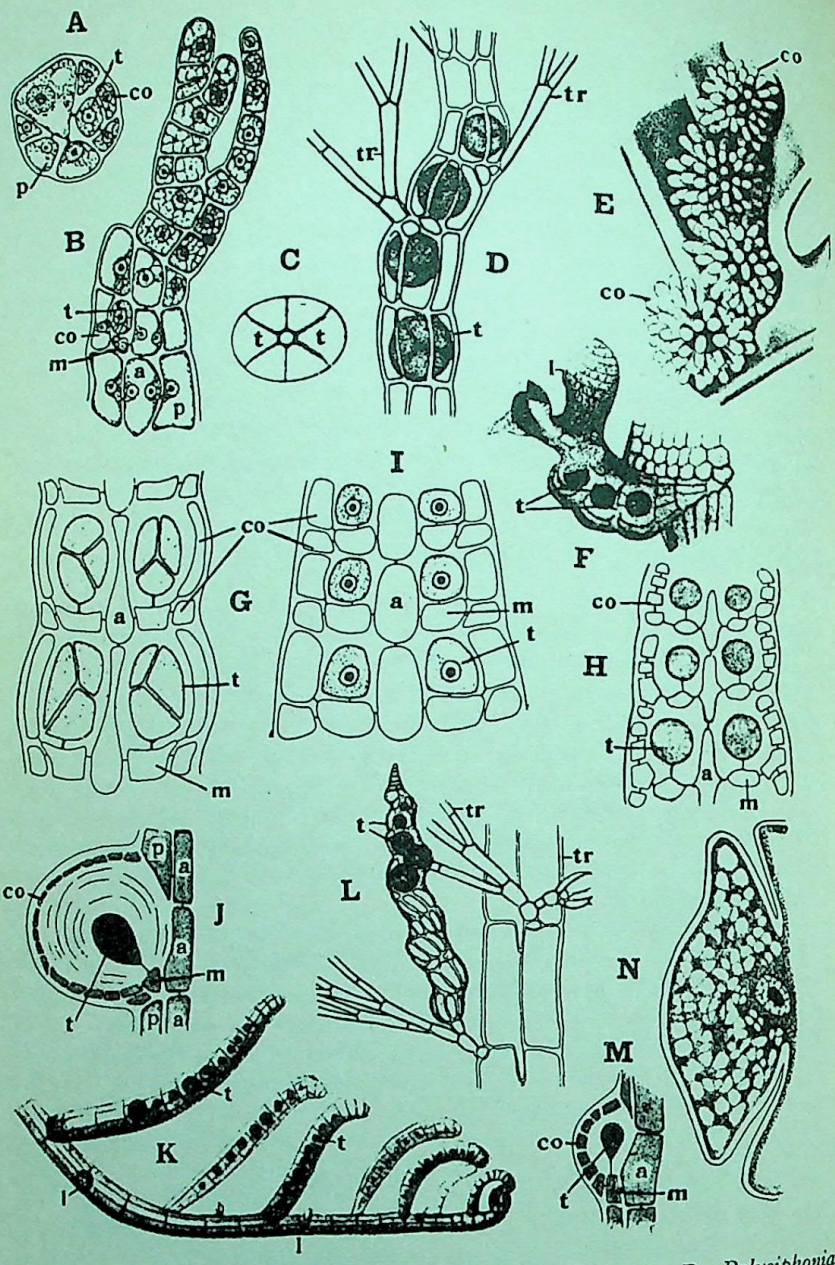

Fig. 291. Tetraspore-formation in Rhodomelaceae. A, B, *Polysiphonia nigrescens* (Huds.) Grev.; A, formation of initial, transverse section; B, the same, apex of a branch-system. C, I, *Odonthalia dentata* (L.) Lyngb.; C, transverse section of young fertile segment; I, longitudinal section, formation of initials. D, *Polysiphonia violacea* (Roth) Grev., stichidium. E, J, M, *Cliftonaea Lamourouxii* Harv.; E, surface-view of part of a mature fertile frond; J, mature and M, young sporangium in section. F, *Leveillea junger-*

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(fig. 210 A, *l*) produces a sporangium (*t*) from one of the dorsal pericentrals. In *C. Lamourouxii* ((192) p. 385) the maturing sporangium acquires a thick hyaline wall (fig. 291 M, J), while the numerous cover-cells (*co*) ultimately grow out into blunt papillae, affording a characteristic picture (fig. 291 E). Similar large sporangia with numerous cover-cells occur in *Leveillea* ((60) p. 355, (192) p. 398), where they occupy 3–5 of the basal segments of arrested long shoots (fig. 291 F). The fertile branches of *Amansia* and *Vidalia* ((192) p. 404) show the same dorsiventrality as the vegetative ones and in the latter are often richly branched; two sporangia are produced in each segment.

(iv) *Dasyaceae.*

The tetrahedrally divided sporangia here also usually occupy special stichidia (fig. 289 F). Those of *Dasya* ((192) p. 617, (547) p. 49) and *Heterosiphonia* ((192) pp. 633, 649, (547) p. 74) are borne on the pseudolaterals (fig. 289 F, *pl*), in the former sometimes also on adventitious branches; the number of pericentrals is five in *Dasya*, 6–7 in *Heterosiphonia*. Each pericentral may produce a sporangium (cf. also (50) p. 317), although one or two are commonly sterile. In *Dasya* (fig. 289 H) the three cover-cells (*co*), cut off after the formation of the sporangium, are small and the latter is left exposed. The stichidia of *Dasyopsis* ((547) p. 60) are mostly formed on adventitious branches and possess six pericentrals.

The repeatedly forked stichidia of *Dictyurus* ((192) p. 680) project freely from the upper edges of the fronds and usually form six sporangia in each segment. In *Thuretia* ((192) p. 672) they are constituted by the swollen bases of lateral sympodia, the upper part of which participates in the formation of the network; the stichidium is enveloped by hyphae and forms sporangia in two alternating rows.

(*c*) *Interrelationships of Ceramiales*

The Ceramiales probably represent an independent series evolved from uniaxial haplobiontic types; there is no satisfactory evidence of a closer affinity with other diplobiontic forms. The Ceramiaceae are no doubt the least specialised members of the order, as shown by a consideration both of the vegetative and reproductive features. Those genera that exhibit whorled branching (*Crouania*, *Antithamnion*) probably come nearest to the ancestral type, not only because this habit is clearly the basic one on which the construction of many

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mannioides (Mart. & Her.) Harv., shoot of unlimited growth with young sporangia. G, N, *Rhodomela virgata* Kjellm.; G, longitudinal section, with mature sporangia; N, undivided sporangium. H, *Bostrychia Hookeri* Harv., longitudinal section with initials. K, *Herposiphonia secunda* (C. Ag.) Falkenb., stichidia. L, *Lophocladia trichoclados* (Mert.) C. Ag., stichidium. *a*, axial cell; *co*, cover-cells; *l*, laterals; *m*, mother-cell of sporangium; *p*, pericentral; *t*, tetrasporangium; *tr*, trichoblast. (A, B, G, I, N after Kylin; D, L after Boergesen; the rest after Falkenberg.)

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Florideae (incl. Ceramiales) is moulded, but also because of the comparative data furnished by the position of the procarp (p. 684). Diverse Ceramiaceae (*Callithamnion*, *Seirospora*, etc.) have, however, lost this habit and indeed exhibit a very simple vegetative structure.

Delesseriaceae and Rhodomelaceae, in their customary possession of four or more pericentrals, no doubt constitute a special development along several distinct lines from such a whorled type. The Rhodomelaceae, in particular, exhibit marked specialisation in the evolution of forms with dorsiventral organisation, accompanied by a tendency towards congenital fusion of branch-systems, resulting in such extreme types as *Pollexfenia*, *Leveillea*, and *Amansia*. Compared with the considerable range in outward form presented by the two families under discussion, there is remarkable uniformity in reproductive features. It is noteworthy that, while in Delesseriaceae and Rhodomelaceae the spores are nearly always tetrahedrally arranged, a cruciate disposition is found in certain Ceramiaceae, and especially in those (*Crouania*, *Antithamnion*) which on other grounds are regarded as the least specialised.

The relation of the Dasyaceae to the other three families is difficult to assess. Falkenberg's view, that forms like them were the starting-point for the evolution of the Rhodomelaceae, has already been considered (p. 576). The only further feature in favour of this view furnished by the reproductive characters is that the gonimoblast in Dasyaceae develops in a more primitive manner than in Rhodomelaceae (p. 709). Rosenberg ((547) p. 82) and Kylin ((397) p. 20) emphasise the resemblances between Dasyaceae and Delesseriaceae, but in view of the marked dissimilarity in vegetative features, it may be doubted whether too much stress should be laid on the reproductive resemblances, since in this respect there is a high degree of uniformity among Ceramiales as a whole. The Dasyaceae are probably best regarded as a separate evolutionary line, parallel with the other three, but rather more obscure in its origins.

Several genera are known which display characteristics of more than one family of Ceramiales. *Lejolisia mediterranea* Born. ((64), (67) p. 148, (478) p. 354, (577) p. 135, (590) p. 116), a small epiphyte (fig. 292 C) in which the creeping filaments (*c*) bear little-branched erect threads (*e*), combines the free (tetrahedral) sporangia of Ceramiaceae with an urceolate cystocarp resembling that of Rhodomelaceae. The envelope consists of closely apposed threads, although these do not actually cohere. According to Feldmann (769) the gonimoblast is like that of *Ptilothamnion*. A peculiar feature lies in the persistence of the trichogyne (*t*) which, during the development of the cystocarp, comes to occupy a lateral position.

A rather different example is provided by *Herpochondria* ((192) p. 215, (599) p. 435), a dorsiventral ally of *Chondria*, in which the

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polysiphonous branches are congenitally fused to form a flat prostrate thallus (cf. *Pollexfenia*, etc.) The free marginal stichidia resemble those of a *Chondria*, and in most other respects too the characteristics are those of a member of Rhodomelaceae. The cystocarps ((490) p. 6,[1] (727) p. 338) are, however, naked like those of most Ceramiaceae.

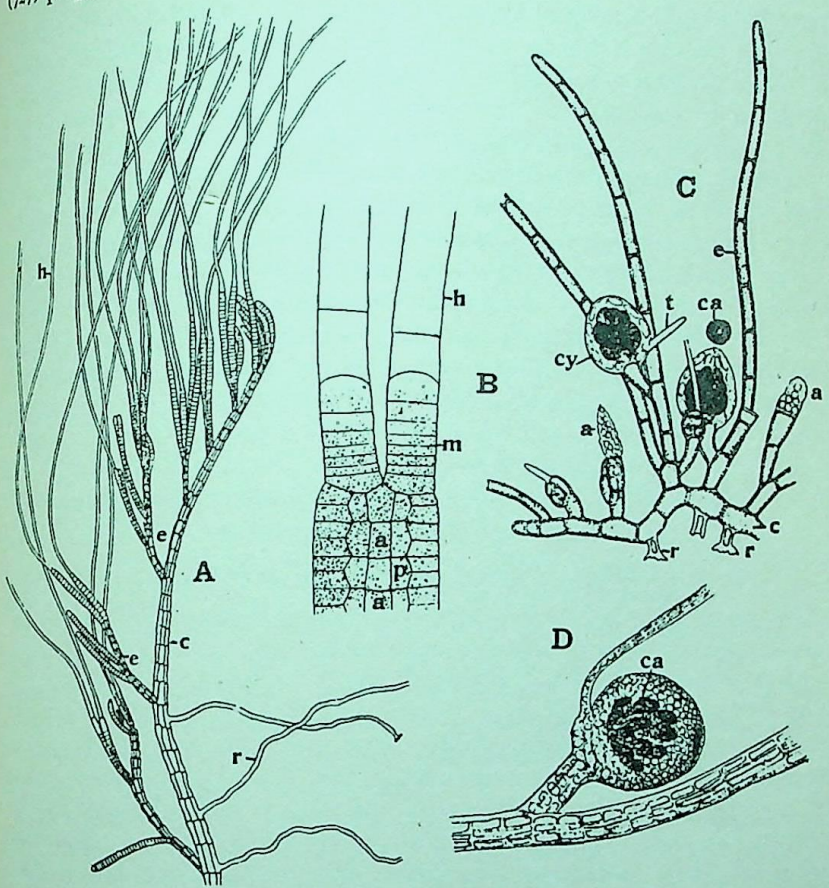

Fig. 292. A, B, *Taenioma perpusillum* J. Ag.; A, habit of part of a plant; B, apex of an erect shoot with hairs. C, *Lejolisia mediterranea* Born. D, *Platysiphonia miniata* (Ag.) Boerges., branch with cystocarp. *a* (in B), axial cells; *a* (in C), antheridia; *c*, creeping branches; *ca*, carposporangia; *cy*, cystocarp; *e*, erect branches; *h*, hairs; *m*, meristem; *p*, pericentral; *r*, rhizoid; *t*, trichogyne. (C after Bornet; the rest after Boergesen.)

Mention may also be made of the Sarcomenieae which appear to constitute a link between Delesseriaceae and Rhodomelaceae. They include *Sarcomenia* ((9) p. 120), *Platysiphonia* ((55), based on *Sarcomenia miniata* J. Ag., cf. (721)), *Taenioma* ((2) p. 1256, (50) p. 338, (68) p. 69,

[1] Okamura suggests the merging of *Herpochondria* in *Microcladia*, for which there are no grounds; it remains doubtful whether he and Falkenberg had the same plant before them ((192) p. 735).

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(192) p. 709, (689), (781) p. 534) and *Cottoniella*[1] ((50) pp. 333, 477, (54) p. 144), the last at present known only in the vegetative condition. These are in general dorsiventral forms with four pericentrals produced in successive pairs, as in Delesseriaceae. The terete creeping branches (fig. 292 A, *c*) bear, on their dorsal side, erect fronds with a tendency to flattening as a result of division of the lateral pericentrals (cf. fig. 292 B); this is very marked in *Sarcomenia delesserioides* Sonder ((277) pl. 121). The flat antheridial branches also resemble those of Delesseriaceae. The urceolate cystocarps of *Taenioma* and *Platysiphonia* (fig. 292 D) are, on the other hand, like those of Rhodomelaceae, although no details are available as to the manner of development of the gonimoblast. The sporangia are formed in two rows in the fertile branches. *Taenioma* (fig. 292 A, B) is distinguished by the long colourless hairs (*h*) with a basal meristem (*m*), that crown the branchlets and show a considerable resemblance to those of Phaeophyceae. In *Cottoniella* the ultimate branches are uniseriate. These diverse genera, which in their vegetative construction approximate so closely to some of the dorsiventral Rhodomelaceae, merit a fuller study than they have so far received.

8. General Consideration of the Life-cycle of the Diplobiontic Florideae

The Distribution of Sexual and Asexual Reproductive Organs

Cytological corroboration of the existence of distinct diploid asexual and haploid sexual phases has now been obtained in a considerable number of diplobiontic Florideae.[2] In Cryptonemiales, Gigartinales, and Rhodymeniales there is usually, despite occasional exceptions (cf. (347) p. 223), a sharp segregation of sporangia and sex organs on separate individuals; among Ceramiales the exceptions are more numerous (cf. p. 723). Spermatia are frequently found attached to the trichogynes, although fusion of the sex nuclei has not often been seen (p. 597). A regular alternation of tetrasporic and sexual individuals has, moreover, been occasionally recorded in nature (see p. 727) and has been established experimentally by Lewis (430) for a number of Florideae. All these facts imply the widespread occurrence of an isomorphic alternation of haploid and diploid phases.

[1] Incl. *Sarcomenia filamentosa* Howe ((314) p. 571).

[2] *Corallina mediterranea* (757) among Cryptonemiales (stages in reduction division also observed in *C. rubens*, (659) p. 45); *Cystoclonium* ((380) p. 30) among Gigartinales; *Lomentaria clavellosa* ((680) p. 23), *Chylocladia* ((740) p. 572), and *Rhodymenia* ((735) p. 158) among Rhodymeniales (cf. also (380) pp. 39, 44, (735) p. 160); *Callithamnion* ((453), (740) p. 567), *Spermothamnion* (179, 606), *Ceramium* ((740) p. 571), *Griffithsia* (375, 428), *Plumaria* (180), *Delesseria* (665), *Phycodrys* ((380) p. 79), *Nitophyllum* (669), *Martensia* (663), *Polysiphonia* ((380) p. 118, (755-6)), *Brongniartella* ((605), (740) p. 567), *Rhodomela* ((371), (740) p. 568), *Laurencia* and *Chondria* ((735) p. 156, (740) p. 569), and *Dasya* ((547) p. 39, (740) p. 570) among Ceramiales.

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It has long been known, nevertheless, that procarps (or carpospores) and tetrasporangia commonly occur on the same individual among Ceramiales,[1] and especially among Ceramiaceae; the form *amphicarpa* of *Callithamnion corymbosum* ((692) p. 69) derives its name from the frequency of this phenomenon. Tetraspores have also been found on male plants (cf. (85) p. 263, (87) p. 298, (89) p. 188, (258) p. 201, (428) p. 671), though, owing to the more temporary character of the male individuals, such instances have been less frequently recorded.

The first example of this association to be fully studied was *Nitophyllum punctatum* (670), in which the fronds often bear both cystocarps and sporangia. The latter (fig. 293 C) are grouped around rudimentary procarps (*t*), which suggests a possible correlation between sporangium-formation and arrest of the procarps. The sporangia develop in the normal manner (p. 716 and fig. 293 J, K); after preliminary multiplication, all but one (*n*) of the nuclei degenerate (*r*). The survivor, however, fails to divide and the entire contents of the sporangium are liberated (fig. 293 D) as a single monospore (*m*); this has the haploid number of chromosomes, although the carpospores of such plants are diploid. In the sporangia found on male plants of *Polysiphonia violacea* ((756) p. 425) and *Griffithsia globifera* ((428) p. 672) the nucleus likewise usually remains undivided, although cleavage furrows, which fail to reach the centre, may appear within the protoplast; occasional stages of nuclear division are observed, but these afford no evidence of meiosis. In *Polysiphonia urceolata* Rosenvinge ((558) p. 410) also records small undivided sporangia on plants with mature cystocarps, while Kylin ((373) p. 83) speaks of aborted sporangia on sexual plants of *Spermothamnion roseolum*. It is thus probable that the sporangia borne on sexual plants usually undergo no reduction and produce only haploid monospores (cf. also (428) pp. 671, 682, (680) p. 6, (782) p. 25).

Spermothamnion affords a common instance of the converse condition ((373) p. 86, (606) pp. 224, 250), viz. of the occurrence of asexual plants bearing normal tetrasporangia side by side with arrested procarps and antheridia. Certain forms of this genus, however, produce tetrasporangia also on a functional sexual phase. Schussnig and Odle ((606) p. 226) state that there is no reduction in such sporangia, but their data are scarcely convincing. They are, moreover, at variance with the conclusions reached by Drew (176), who in *S. Turneri* established the occurrence of meiosis in tetrasporangia found on plants bearing developing gonimoblasts and mature fruits, as well as antheridia. The individuals in question are therefore diploid (with 60

[1] In addition to the instances specially dealt with in the following, see (85) p. 265, (89) p. 189, (283) p. 130, (347) p. 224, (373) p. 83, (380) p. 55, (453) p. 5, (543), (558) pp. 304, 400, (577) p. 136, (736) p. 200. In diverse instances tetrasporangia have actually been found arising from cells of the procarp (cf. (176) p. 552, (593) p. 278, (736) p. 200) or among the gonimoblasts ((737) p. 355).

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chromosomes). Their tetraspores germinate normally. Evidence was obtained ((176) p. 559) that the procarps of these plants were diploid and their gonimoblasts tetraploid;[1] many of the procarps, however, failed to develop further and fertilisation was not directly observed. The probable existence of triploid carpospores, such as would result from the fertilisation of a diploid carpogonium by a haploid spermatium, was also established. Haploid plants, bearing functional sex organs and occasional sporangia which remain undivided, have recently been described by Drew (782), as well as sterile triploid plants. Mathias ((453) p. 20) found tetrasporangia exhibiting reduction and fruits on the same individual also in *Callithamnion brachiatum*, although here the carpospores are stated to be diploid.

The occasional occurrence of tetrasporangia on the sexual plants of the haplobiontic Nemalionales (p. 625) warrants the supposition that this characteristic organ of Florideae evolved prior to the establishment of the diplobiontic life-cycle. There is also increasing reason to believe that the mere presence of tetrasporangia is no proof of the diploid character of the individual on which they occur. It seems probable that, when an isomorphic alternation was first established by postponement of meiosis (cf. p. 627), each of the two phases still bore tetrasporangia, although reduction was associated only with the sporangia of the one phase; it is possible that this phase for a time still possessed functional or functionless sex organs. The persistence of abortive sex organs on the diploid, and of monospore-producing sporangia on the haploid, phase would on this view be tokens of an ancestral condition and would mark a more primitive state than the sharp individualisation of the two phases that characterises many diplobiontic Florideae. It is noteworthy in this connection that the simultaneous presence of sex organs and sporangia is more frequent in the relatively primitive Ceramiaceae (p. 723) than in the more specialised families of Ceramiales (cf. also (771) p. 552).

In the light of this hypothesis *Spermothamnion* may perhaps be regarded as a form in which sex organs have persisted on the diploid stage and in certain instances remained functional (cf. also (176) p. 567), although they may also have secondarily reacquired their former function. However that may be, the possibility for the origin of tetraploid and triploid races afforded by such phenomena is of considerable importance, and the further investigation of these matters will be awaited with interest.

In several Florideae (*Acrosymphytum*, *Thuretella*, *Thuretellopsis*, *Halarachnion*, *Gigartina stellata*) tetrasporangia are so far unknown. It is possible that they are produced on dwarf plants ((347) p. 221) which remain at the juvenile stage, since such stages occasionally bear tetra-

[1] Cf. the criticisms of Svedelius ((680) p. 6). I have had an opportunity of examining some of Drew's preparations and believe that there is a considerable degree of foundation for her views.

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sporangia (fig. 159 D, *sp*; Kuckuck's prospory, (363) p. 196). Berthold ((36) p. 421) comments on the abundance of dwarf fertile plants in the Mediterranean (cf. also (226) p. 402).

On the other hand, some of these seaweeds may be parthenogenetic, with a gonimoblast producing haploid carpospores, although Oltmanns observed spermatia on the trichogynes of *Acrosymphytum* (fig. 240 C, *G, s*), and there is little evidence for the occurrence of parthenogenesis in Rhodophyceae.[1] A commonly accepted instance is furnished by *Platoma* (p. 657), where male organs are unknown ((363) p. 191) and occasional cruciate tetrasporangia occur on the female individuals, but this still awaits cytological investigation. Rosenvinge ((558) pp. 169, 179) records the development of gonimoblasts from carpogonia of *Furcellaria fastigiata* and *Petrocelis Hennedyi* lacking all traces of spermatia on the trichogynes. These may be instances of actual parthenogenesis, or autogamy may replace normal fertilisation. Attention may also be drawn to the apparent non-existence of female individuals in the common *Rhodymenia palmata* ((169) p. 329, (558) p. 575) which probably indicates an abnormal life-cycle. The same is true of *Antithamnion boreale* ((558) p. 370).

Tetrasporic and sexual individuals of the same species are often unequally represented in nature. Among Cryptonemiales and Gigartinales there are several records indicating a preponderance of sexual individuals ((387) p. 35, (526) p. 254, (532) p. 68, (558) pp. 174, 281, (659) p. 30); tetrasporic plants of *Gloeosiphonia capillaris* occur on the coasts of Holland ((253) p. 51), but not on those of France or Denmark ((558) p. 278). Among Ceramiales the available data[2] indicate the reverse condition, sexual individuals often being scarce. There is some evidence that this depends on temperature-conditions and probably also on other factors of the habitat (243); thus, Levring ((426) p. 142) reports only tetrasporic plants of *Callithamnion Furcellarieae*, *Polysiphonia nigrescens*, and *Rhodomela subfusca* in the waters of the Baltic with their low salinity. On British shores *Spermothamnion roseolum* is represented only by tetrasporic individuals. Many investigators comment on the more robust character of the asexual individuals in Ceramiales (cf. also (578) p. 50).

In *Trailiella*, *Antithamnionella*, *Lomentaria rosea*, and *Dasya ocellata* Harv. only tetraspores have so far been found[3] (cf. also *Hildenbrandia*, p. 655). Svedelius (680) has established that in *Lomentaria rosea*, a northern species always found in water of considerable depth, the tetraspores have the same number of chromosomes as the vegetative cells. Comparison with other species of *Lomentaria*, having a normal life-cycle, shows that the plants of

[1] The parthenogenesis in *Ptilota* suggested by Davis ((163) p. 375) is probably unfounded (cf. (380) p. 61, (518) p. 365).

[2] Cf. (50) p. 205, (75) p. 4, (375), (426) pp. 94, 112, (428) p. 640, (517) p. 186, (519) p. 186, (558) pp. 343, 367, (736) p. 201; see also *Furcellaria* ((532) p. 116).

[3] Miranda ((462) p. 378), however, describes antheridia in *Antithamnionella*.

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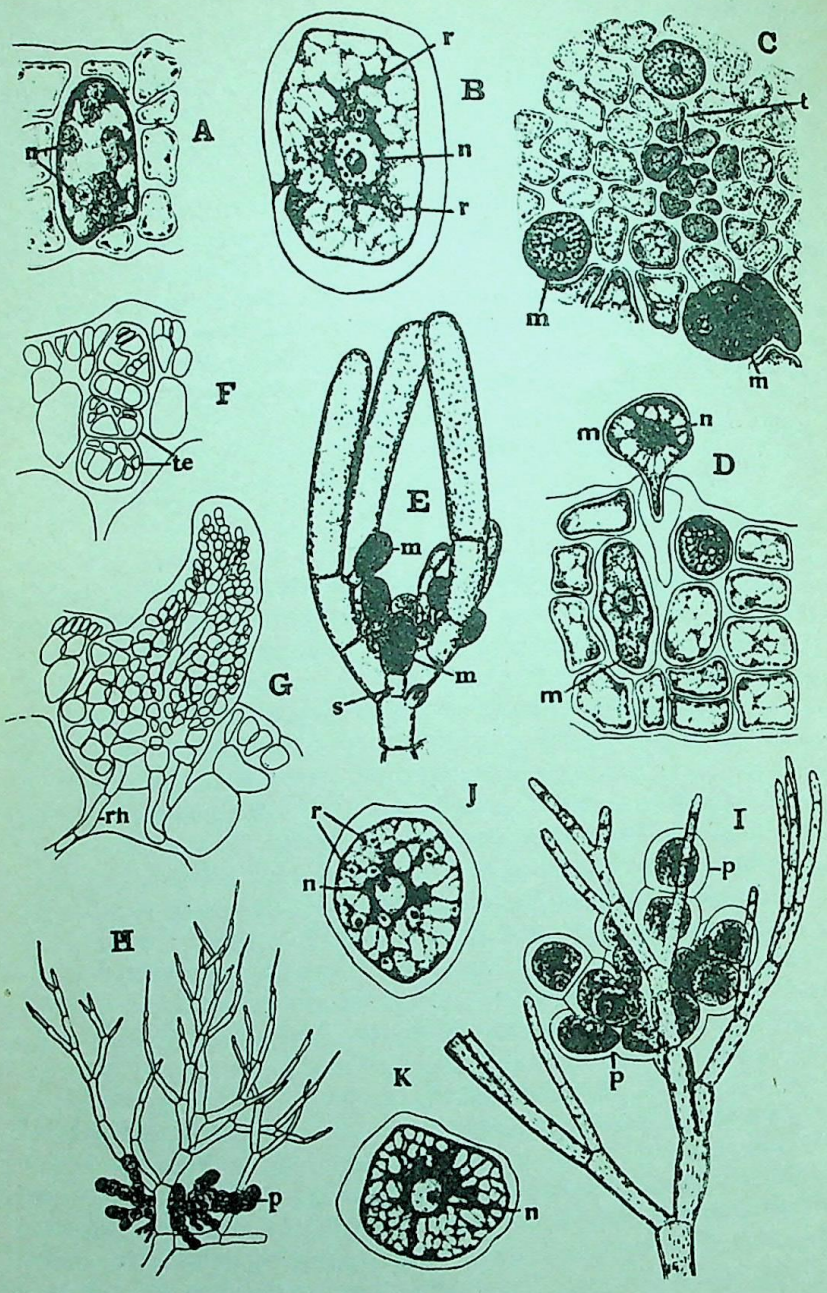

Fig. 293. A–D, J, K, *Nitophyllum punctatum* (Stackh.) Grev.; A, B, successive stages in development of normal tetrasporangium from a diploid plant, in B showing supernumerary nuclei (*r*) and the functional nucleus (*n*); C, D, monospore-formation and liberation on the haploid plant; J, K, successive stages in development of monosporangium. E, *Monospora pedicellata* (Smith)

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L. rosea are diploid, so that in this species the sexual phase has probably[1] been lost. In *Dasya ocellata* also Westbrook ((740) p. 571) failed to obtain good evidence of the occurrence of meiosis in the tetrasporangium.

In certain Florideae (especially Ceramiales) inhabiting northern waters, the sexual individuals tend to be largely summer-forms, while it is the asexual ones that last through the winter. Such instances are not without interest in relation to the problem of the origin of purely diploid types. Lewis (431) found that at Woods Hole *Dasya pedicellata*, *Griffithsia globifera*, and *Polysiphonia violacea* form carpospores in August and that the resulting tetrasporic plants pass through the winter as small germlings, which mature their tetraspores in July; many of the Red Algae in this region are believed to show a similar seasonal cycle. Comparable data are furnished by Kniep ((347) p. 220) for *Laurencia hybrida* and by Svedelius (676) for *Ceramium corticatulum* in the Baltic (cf. also (184), (558) p. 433). Similarly, there is a preponderance of tetrasporic plants of *C. rubrum* in winter and of cystocarpic ones in summer in the Isle of Man ((348) p. 117). In other localities, however, the same species may show a different behaviour (cf. e.g. (431) p. 34 for *C. rubrum*; (635) for *C. corticatulum*).

These are by no means the only data indicating a certain seasonal succession (cf. e.g. (226) pp. 380, 382, 448, etc.; (707), (776) for the Mediterranean), but in most other instances this is not very clearly marked. Abundant records (cf. (427), (532), (676) p. 21), moreover, testify to the frequent simultaneous occurrence of the two phases, although sometimes the one and sometimes the other persists for a longer period. The sequence may, moreover, be reversed; thus, *Ceramium tenuissimum* bears cystocarps from April to June and tetraspores from then till August, while in *Dumontia incrassata* ((183) p. 435, (535) p. 238) sexual plants are found in the early part of the year and tetrasporic ones later on. On North European coasts cystocarpic plants of *Harveyella* are found in winter and the tetrasporic ones mainly in spring ((657) p. 29).

In *Agardhiella* Osterhout ((505) p. 419; cf. also (347) p. 234) describes the outgrowth of the entire contents of a tetrasporangium as a single structure; for a time (fig. 293 F) the groups of cells derived from the separate spores (*te*) remain distinguishable, but by degrees the limits become obscured. The base of the single proliferation thus produced (fig. 293 G) is embedded in the parent-thallus and the lower cells

[1] Segawa ((608) p. 185) records an individual with cystocarps, but it is not certain that the same species is involved ((680) pp. 22, 36).

Sol., monospore-formation. F, G, *Agardhiella tenera* (J. Ag.) Schmitz, germination of tetraspores in situ, with formation of a single plant; F, young and G, older stages. H, *Seirospora occidentalis* Boerges. and I, *S. Griffithsiana* Harv., paraspore-formation. *m*, monospore; *n*, nuclei; *p*, paraspores; *r*, supernumerary nuclei; *rh*, rhizoid; *s*, stalk-cell; *t*, trichogyne; *te*, tetraspores. (E after Bornet & Thuret; F, G after Osterhout; H after Boergesen; I after Rosenvinge; the rest after Svedelius.)

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give rise to penetrating rhizoids (*rh*). These growths bear male or female sex organs or more rarely tetrasporangia ((167) p. 507); the presence of the last may imply an absence of reduction. Osterhout mentions the occurrence of comparable proliferations in *Cystoclonium* (cf. also (558) p. 593) and *Gracilaria*. Other instances are known in *Champia parvula* ((486) p. 164) and *Lomentaria rosea* ((680) p. 19), in the latter associated with diploid tetraspores (cf. p. 725). The example afforded by *Agardhiella* is of particular interest because, when the proliferations bear sex organs, the sexual phase is parasitic on the asexual one, and we have the converse condition to that found in diverse Gigartinales (cf. p. 731).

Special Types of Asexual Reproduction

The Ceramiaceae frequently produce special types of reproductive cells which are restricted to the asexual individuals. As a general rule these also bear tetrasporangia, although in certain species the latter are lacking on most individuals. *Monospora*[1] *pedicellata* (*Callithamnion pedicellatum* C. A. Ag. (68) p. 21, (118), (276) pl. 212, (478) p. 372, (580) p. 203) owes its generic name to the customary production of ovoid "monosporangia" (fig. 293 E, *m*), accompanied by infrequent tetrasporangia with tetrahedral spores; sexual plants are rare and have not been found on British shores. The "monosporangia", which are deeply pigmented and multinucleate, occupy the same position as the tetrasporangia and are seated on a stalk-cell (*s*) with scanty contents. At maturity they become detached as a whole and germinate without shedding the enveloping membrane; a further sporangium can develop from the same stalk-cell. In view of the variable size of the latter, Schiller ((580) p. 204) regards the structures under discussion as bisporangia in which the lower cell has degenerated. Although probably diploid ((400) p. 159), the detachment and germination of the entire organ renders its sporangial nature doubtful.

The so-called paraspores of *Seirospora Griffithsiana*[2] ((68) p. xiv, (478) p. 364, (580) p. 144, (593) p. 276), which may be associated with bi- and tetrasporangia ((129) p. 217, (209) p. 11, (432) p. 195), occur as branched tufts (fig. 293 H, I, *p*), composed of rounded thick-walled uninucleate cells; in *S. occidentalis* ((50) p. 225) they occupy the same position as the sporangia. The individual cells become detached at maturity, but the contents escape from the membrane prior to germination ((558) p. 351). Similar structures are recorded at the tips of the branches of *Ceramium strictum* ((580) p. 148) and *C. Deslongchampii* ((253) p. 45). Spermatia have been observed on the trichogynes of *Seirospora Griffithsiana* ((460) p. 284) so that this species probably

[1] *Neomonospora*, according to Setchell & Gardner, *Proc. California Acad. Sci.* IV, **22**, 87, 1937.

[2] Cf. also *Dohrniella* ((225) p. 232).

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possesses a normal alternation, the paraspores constituting an accessory means of propagation of the sporophyte. It may be doubted whether they have any homologies with the sporangia. In another species of *Seirospora* they have been found on individuals bearing aborted procarps ((226) p. 468).

Structures described as *polyspores*, which are formed within definite sporangia and have already been noted in *Acrochaetium* (p. 625), are of frequent occurrence among Ceramiaceae (see (737) p. 360) and are also recorded in *Gonimophyllum* ((619) p. 394) and in *Chylocladia* (458). The sporangia of *Gonimophyllum* ((382) p. 96) develop like those of other Nitophylleae (fig. 294 H). The nucleus of the initial divides into 30–50 parts, and the subsequent cytoplasmic cleavage results in a radial group of polyspores (fig. 294 I, *p*) surrounding a central cell (*ce*). In this instance the polyspores appear to replace the tetraspores. This is also so in *Pleonosporium*,[1] in *Spermothamnion Snyderae* among Ceramiaceae, and in *Coeloseira* ((309) p. 871) among Champiaceae. The sexual individuals of *Pleonosporium* bear sex organs closely resembling those of *Callithamnion* ((210), (590) p. 116). The contents of the polysporangium first segment into four and then divide to form 8–24 spores. There is evidence of meiosis ((458) p. 194) and this, taken in conjunction with the details of development, justifies the view ((179) p. 474, (400) p. 157, (558) p. 399) that the polyspores are derivatives of tetraspores. In *Spermothamnion Snyderae* (179) there is a normal alternation (fig. 294 B, C), although the asexual individuals bear polysporangia only. Their initials (fig. 294 E, *sp*) contain several diploid nuclei, which undergo simultaneous meiotic divisions (fig. 294 F, G) so that the resulting spores are in multiples of four.

In most Ceramiaceae, however, the polysporangia are accompanied by tetrasporangia, although the former tend to predominate in certain (colder?) habitats; sexual plants are often rare ((558) p. 400, (660)). The polysporangia usually contain two or more nuclei at an early stage and the spores are mostly formed in multiples of four. They have been recorded in diverse species of *Ceramium* ((513) pp. 51, 85, (524) p. 287, (580) p. 148), where they appear as large spherical structures projecting from the cortical bands (fig. 294 D), in *Callithamnion* ((369) p. 153, (558) p. 311, (734) p. 166), where they occupy the same position as the tetrasporangia (fig. 294 A), and in *Spermothamnion* ((54) p. 16, (478) p. 411, (606) p. 224, (779)). They are also found in *Antithamnion plumula* ((580) p. 146, (593) p. 285) and in *Compsothamnion* ((89) p. 188, (737) p. 360); in the former the number of spores is very considerable, in the latter there are eight. In *Plumaria elegans* ((87) p. 303, (380) p. 58, (531) p. 32, (558) p. 355, (660)) they occupy the tips of

[1] See (21) p. 35 (as *Corynospora*), (60) p. 336, (383) p. 57, (459), (478) p. 399, (580) p. 204. Funk ((226) p. 466) appears to be the only person who has recorded tetraspores in *Pleonosporium*.

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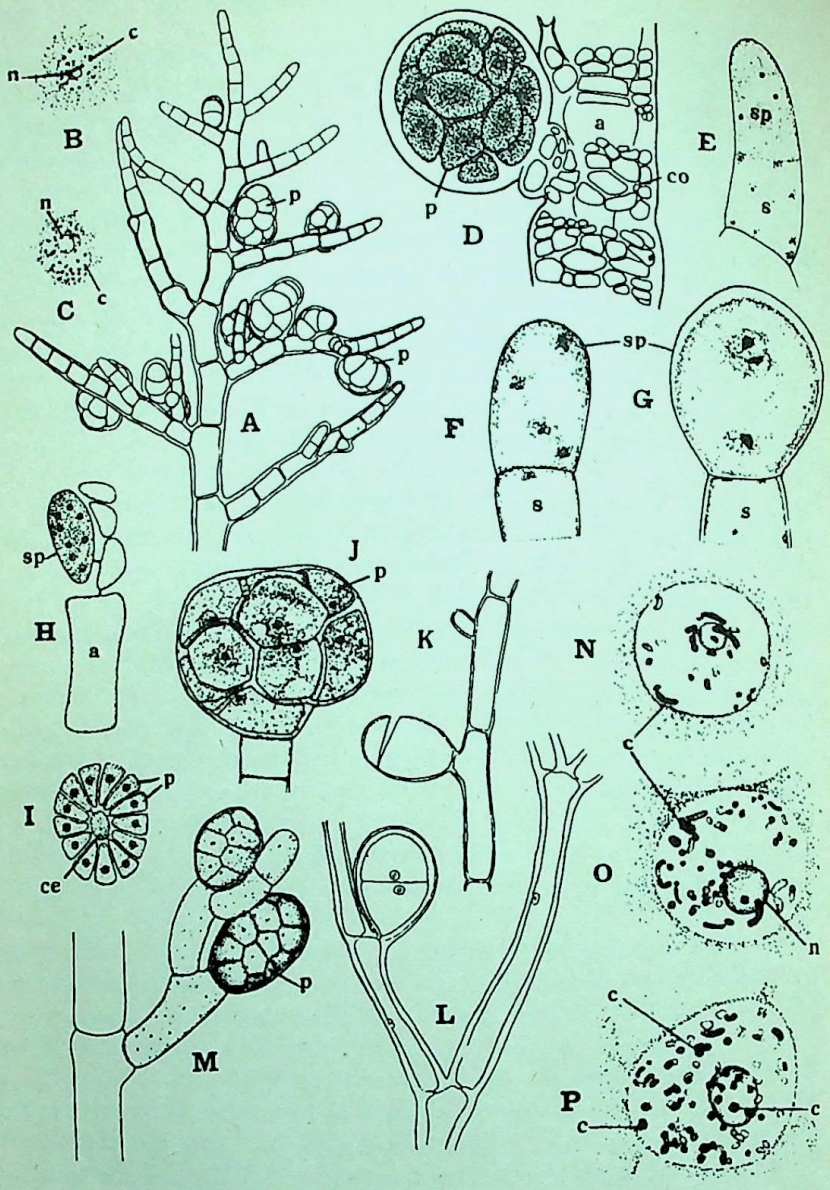

Fig. 294. Polyspores. A, *Callithamnion Hookeri* (Dillw.) Ag. B, C, E–G, *Spermothamnion Snyderae* Farl.; B, nucleus from somatic cell of female plant (haploid); C, the same from a polysporangium (diploid); E, polysporangium-initial, the sporangium (*sp*) about to be cut off; F, young sporangium, nuclei in synezesis; G, the same, diakinesis. D, *Ceramium Deslongchampii* Chauv. H, I, *Gonimophyllum Skottsbergii* Setch.; H, formation of initial; I, mature sporangium in section. J, M–P, *Plumaria elegans* (Bonnem.) Schmitz; J, mature sporangium; M, branch with polysporangium; N, nucleus of apical cell of female plant; O, ditto of tetrasporic plant; P, ditto of plant bearing polysporangia. K, L, *Callithamnion Furcellarieae* J. Ag., bisporangia, in K dehisced. *a*, axial cell; *c*, chromosomes; *ce* (in I), central cell of polyspore-group; *co*, cortex; *n*, nucleolus; *p*, polyspores; *s*, stalk-cell; *sp*, sporangium. (A, D, K, L after Rosenvinge; H, I, M after Kylin; the rest after Drew.)

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the ultimate branches (fig. 294 J, M) and are usually found on distinct plants ((180) p. 349).

In all the instances just mentioned it remains doubtful whether the polysporangia are, as in *Spermothamnion Snyderae*, modified tetrasporangia producing haploid spores, or accessory reproductive organs, the spores of which serve merely for vegetative propagation and are formed without reduction ((400) p. 159, (558) p. 312 et seq., (734) p. 166). A recent investigation by Drew (180) of *Plumaria elegans* has shown that here the polysporangia occur on special triploid plants (cf. fig. 294 P). The spores (fig. 294 J) are formed by successive division of the uninucleate initial and no reduction occurs during their formation. There are also haploid sexual (fig. 294 N) and diploid asexual (fig. 294 O) plants which follow a normal diplobiontic cycle. The mode of origin of the triploid plants is not yet clear, although the probable occurrence of triploid carpospores in *Spermothamnion Turneri* ((176) p. 563) indicates one way in which this condition could be reached. It remains to be seen whether a special nuclear constitution is associated with the occurrence of polysporangiate individuals also in other Ceramiaceae. It can hardly be doubted that the polysporangia are homologous with tetrasporangia, although those of *Plumaria elegans*, and probably of other Ceramiaceae, have undergone more profound modification than those of *Spermothamnion Snyderae*; this perhaps justifies the use for them of the distinctive term *parasporangia*.

Brief reference may be made to the *bispores*, which are particularly frequent in Corallinaceae (p. 655) and also of common occurrence in certain Ceramiaceae (fig. 294 L, and p. 714). Bauch ((35) p. 366), who gives a list of all the records to date, refers to a seasonal alternation between bispore- and tetraspore-producing plants in *Crouania attenuata*. Although an homology with tetrasporangia appears undoubted (216,415), it still remains to be established whether or not reduction occurs in the bisporangium.

Modified Life-cycles

While the previous considerations afford evidence of occasional modifications in the diplobiontic cycle, it is among Phyllophoraceae (Gigartinales) that the most fundamental changes are encountered. Although diverse species of *Phyllophora* possess a normal diplobiontic life-cycle (cf. p. 669 and (522) p. 251), it is now conclusively proved that that of *P. Brodiaei*[1] shows a striking abbreviation ((389) p. 27, (558) p. 525, (563) p. 13). The sex organs (cf. also (158) p. 29, (159) p. 257) occur either on the undulate margins of the fronds (cf. fig. 295 A) or in special marginal leaflets (fig. 295 B, *f*); male and female

[1] The cystocarps described by Darbishire belong, according to Rosenvinge ((563) p. 7), to *P. membranifolia*.

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organs are often found in close association. The procarps (fig. 295 C) resemble those of *P. membranifolia*, but occasionally the trichogyne is scarcely developed. Spermatia have not been observed on the trichogynes, but Kylin ((389) p. 28) records the fusion of carpogonium and supporting (auxiliary) cell (fig. 295 D) which is taken as evidence of fertilisation. The gonimoblast-threads (fig. 295 E, *g*), which arise from the enlarged and multinucleate auxiliary cell (*su*), penetrate in all directions between the cells of the gametophyte with which they establish pit-connections. A considerable number grow towards the exterior and give rise to nemathecial threads (*n*; cf. also (135) p. 546).

As these develop (fig. 295 G, *n*), they raise the overlying cortex (*c*) and penetrate the surface in several places, often on both sides of the parent-frond; the resulting cushions later fuse to form a large globular nemathecium (fig. 295 A, B, *n*), which sometimes encircles an entire fertile leaflet. Several months elapse before the nemathecia commence to form spores. They are differentiated (fig. 295 F) into a medulla (*me*) and a cortex composed of radiating threads (*sp*), in which all the cells, except for the outermost three or four, develop into cruciate tetrasporangia (cf. the nemathecia of other species, p. 674). Since the nemathecia of *P. Brodiaei* arise directly from the gonimoblasts and produce tetraspores, they clearly represent the sporophyte, which is here parasitic on the gametophyte, the carposporangial stage being suppressed. The tetraspores grow into young plants ((558) p. 530, (563) p. 30) which are sufficiently like the mature gametophyte to complete the picture of the life-cycle. Claussen (135) produces rather inconclusive evidence that the nemathecial nuclei are diploid.

The nemathecia just described have been regarded as belonging to a parasite (*Actinococcus subcutaneus* (Lyngb.) Rosenv.; cf. (159), (252), (302), (591) p. 372), which was believed to obtain access through the apertures of the antheridial depressions (fig. 295 H). There were not wanting, however, suggestions that the "parasite" might represent the actual sporophyte of *P. Brodiaei* ((158) p. 12, (554) p. 34), although this remained in doubt until it was established by Rosenvinge. Similar "parasites" are recorded in diverse other species of *Phyllophora* ((522) p. 251), in all of which no asexual individuals are known, while of the "parasite" only tetraspore-producing stages have been found.[1] There is thus considerable presumptive evidence that these species possess an abbreviated life-cycle, comparable to that of *P. Brodiaei*.

An analogous condition is met with in *Gymnogongrus*. *G. norvegicus* is probably a normal diplobiont, since separate cystocarpic and tetrasporic individuals are known; the sporangial nemathecia were at one time regarded as a parasite, *Colacolepis*[2] *peltaeformis*. The tetraspores from these nemathecia, however, germinate like the carpospores of the

[1] Heydrich's carpogonia do not exist.

[2] *Colacolepis* was distinguished from *Actinococcus* by the shallow penetration of the endophytic threads, from which the nemathecium was supposed to originate.

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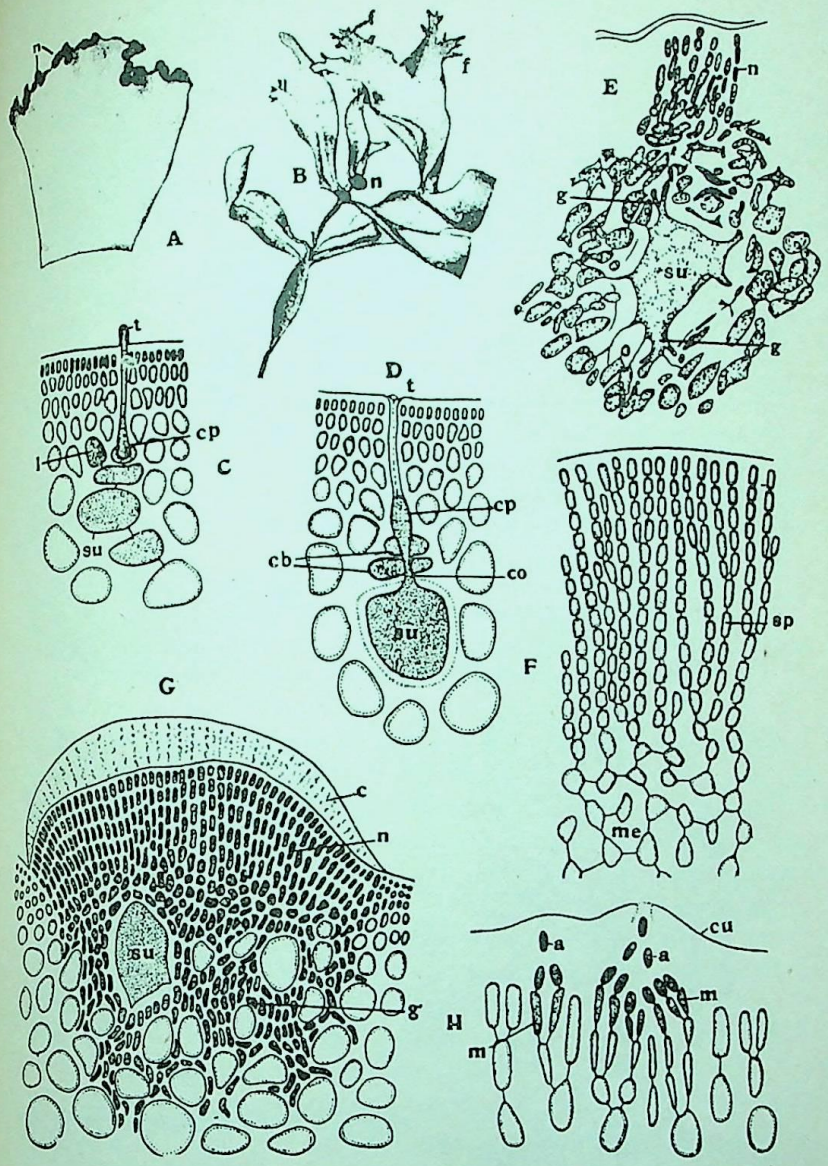

Fig. 295. *Phyllophora Brodiaei* (Turn.) J. Ag. A, B, plants with nemathecia (*n*); C, procarp; D, fusion between carpogonium and supporting (auxiliary) cell; E, development of gonimoblast; F, G, sections of young nemathecia; H, antheridial development. *a*, antheridium; *c*, cortex; *cb*, carpogonial branch; *co*, connecting filament; *cp*, carpogonium; *cu*, cuticle; *f*, fertile fronds; *g*, gonimoblast; *l*, lateral; *m*, antheridium mother-cell; *me*, medulla; *n*, nemathecia and nemathecial threads; *sp*, young sporangia; *su*, supporting cell; *t*, trichogyne. (A, B, E after Rosenvinge; the rest after Kylin.)

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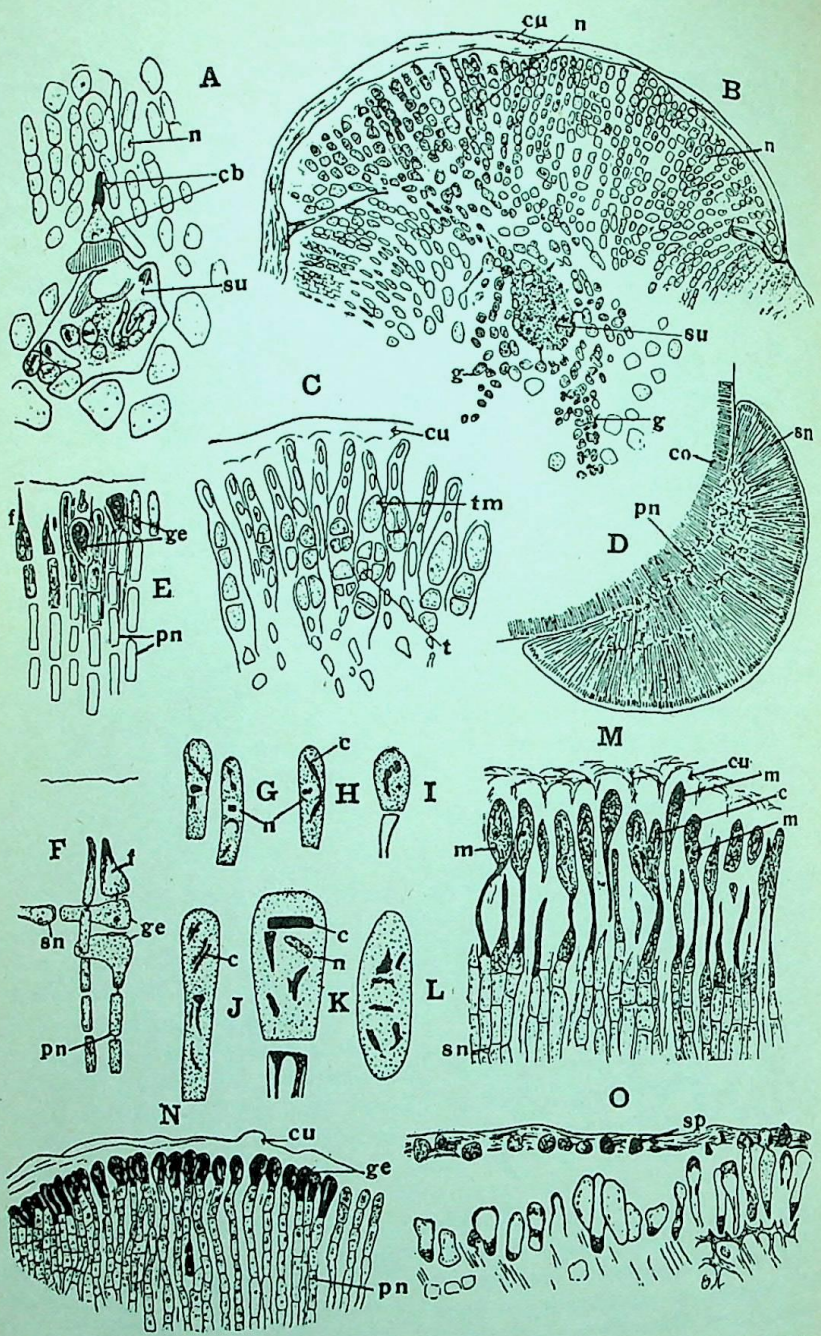

Fig. 296. A–C, *Gymnogongrus Griffithsiae* Mart.; A, older procarp; B, transverse section through developing nemathecium; C, spore-producing threads. D–O, *Ahnfeltia plicata* Fries; D, section of older nemathecium (diagrammatic); E, a few threads from a young nemathecium; F, development of secondary nemathecial threads; G–L, details of monospores; M, transverse

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cystocarpic individuals (107,123) and produce erect fronds, having the structure of a *Gymnogongrus*. *G. linearis* (Turn.) Ag. also forms normal cystocarps ((174), (404) p. 26), although no tetrasporic individuals are known; spermatia have been observed on the trichogynes.

In many species of *Gymnogongrus*, however, cystocarps are lacking (cf. (522) p. 250), and this is so in *G. Griffithsiae*. The "parasite" (*Colacolepis aggregatus*), found on this species, bears the same relation to the procarp as in *Phyllophora Brodiaei* ((255), (256) p. 532), while its spores produce germlings with a discoid base bearing *Gymnogongrus*-fronds (128). Antheridia are unknown in *G. Griffithsiae*, and there is no evidence that fertilisation occurs. The procarps (fig. 296 A) are rudimentary and possess a large supporting cell (*su*), bearing a two-celled carpogonial branch (*cb*; cf. also (128) p. 759). Numerous threads (fig. 296 B, *g*) arise from the supporting cell and some of them combine to form a fan-shaped mass of tissue (*n*), which penetrates the surface and forms a lobed nemathecium. There is no sharp line of demarcation between its cells and the cortical tissue of the parent. The nemathecia, which are generally situated near the bifurcations of the thalli, form chains of sporangia (fig. 296 C) producing either tetra- or monospores (255).

Another instance is furnished by *G. platyphyllus* Gardn. ((235) p. 247), in which the "parasite" (*Actinococcus chiton* Howe) has been shown (174) to be the tetrasporic stage. This arises in essentially the same way as in *G. Griffithsiae*; antheridia are again unknown. It is possible that these species are altogether haploid.

Despite its abundance, cystocarps have never been recorded in *Ahnfeltia plicata*.[1] Especially during winter, however, the plants commonly bear yellowish nemathecia producing monospores ((87) p. 302), which were long regarded as belonging to a parasite *Sterrocolax decipiens* Schmitz ((591) p. 393), although their independence was sometimes questioned. Rosenvinge ((558) p. 560, (564) p. 4) provided the proof that these nemathecia are part of the reproductive cycle of *Ahnfeltia* (cf. also (125), (255), (256) p. 534). No procarps are present, and the nemathecia (fig. 296 D) arise merely by proliferation of the cortical cell-rows (*co*) of the thallus. According to Rosenvinge[2] the primary nemathecial filaments (*pn*) bear two kinds of cells, viz. (*a*) terminal flask-shaped ones (fig. 296 E, *f*), possibly representing hairs,

[1] The male organs (fig. 296 O) described by Gregory ((256) p. 547) require further investigation.

[2] Gregory has a slightly different interpretation.

section of mature nemathecium, development of monospores; N, ditto of developing nemathecium before production of the secondary threads; O, development of antheridia(?). *c*, chromatophore; *cb*, carpogonial branch; *co*, cortex; *cu*, cuticle; *f*, flask-shaped cells; *g*, gonimoblast; *ge*, generative cells; *m*, monosporangium; *n*, nucleus; *pn*, primary and *sn*, secondary nemathecial threads; *sp*, spermatium(?); *su*, supporting cell; *t*, tetraspore; *tm*, tetrasporangium mother-cell. (A–C, M–O after Gregory; the rest after Rosenvinge.)

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and (*b*) so-called generative cells (*ge*) which have dense cytoplasmic contents and are either terminal or situated laterally on the end-cells (fig. 296 N, *ge*). The generative cells, which are regarded as reduced procarps, give rise to threads (fig. 296 F, *sn*) which, extending outwards, produce a system of secondary nemathecial filaments (fig. 296 D, *sn*) overlying the primary ones and spreading over the surface of the parent-thallus. The end-cells of these threads (fig. 296 M) constitute the monosporangia[1] (*m*; cf. also fig. 296 G–L). Gregory ((256) p. 547) records fusions between the medullary cells in the neighbourhood of a nemathecium. Rosenvinge concluded that the number of chromosomes was the same in the medullary cells and in the monospores (cf. however (255) p. 768), but, although this is probable, there is need for a careful cytological study.

The monospores germinate like those of *Gloeosiphonia* (p. 461; (125) p. 350). The resulting violet-coloured crusts bear hyaline hairs and closely resemble the basal discs of *Ahnfeltia* (cf. also (77) p. 287).

The life-cycle of *Ahnfeltia* thus presents a further stage in the reduction-series afforded by *Phyllophora Brodiaei* and *Gymnogongrus Griffithsiae*. The condition existing in *P. Brodiaei* shows a marked degree of correspondence with that found in *Liagora tetrasporifera* and *Helminthocladia Hudsoni* among Nemalionales (p. 627) and constitutes a striking example of convergent development. In either instance, although the starting-point is quite different, a probable diploid phase dependent upon the haploid one is attained. The relation of the one to the other is altogether comparable to that found in Bryophyta. The manner of origin of such a dependent phase is of such interest that it is to be hoped that a thorough cytological investigation of these particular Florideae will not be long outstanding. Until then the actual state of affairs remains conjectural.

The condensed life-cycle of the Phyllophoraceae just considered naturally raises the question of the relation between the haplobiontic and diplobiontic types. A species like *Gymnogongrus Griffithsiae* is probably haploid throughout its life-cycle, and it is possible to conceive of the origin of a typical haplobiont by a comparable process of condensation. If, however, the haplobiontic Florideae be regarded as derived from diplobiontic types ((133) p. 329), a general simplification must be assumed to have taken place concurrently, for in almost every respect (chromatophores, thallus-structure, carpogonial branches, usual absence of auxiliary cells, etc.) the majority of Nemalionales appear as less specialised than the diplobiontic forms (cf. (678) p. 45). There is, moreover, presumptive evidence of a postponement of the reduction divisions in species of *Liagora* and *Helminthocladia*, whereas there are no facts indicating a transference of the seat of reduction from the tetrasporangium to the zygote. The Phaeophyceae demonstrate how tenaciously the place of the reduction

[1] De Toni's record of tetraspores ((705) p. 204) is probably erroneous.

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divisions may be confined to a definite type of reproductive organ (the unilocular sporangium).

Attention may also be drawn to the instances afforded by Ulvaceae and Cladophoraceae among Chlorophyceae (1, pp. 216, 241), where likewise postponement of meiosis and establishment of isomorphic alternation is associated with advance in vegetative organisation ((771) p. 536). Svedelius ((675), (677) p. 375, (678) p. 48) has emphasised the advantages arising from a postponement of reduction from the zygote to the sporangia of a distinct phase. The single division in the zygote is replaced by a large number of separate meiotic divisions upon the diploid phase, so that the possibilities for the redistribution of the characteristics of the parent are indefinitely multiplied.

If the zygote of a haplobiontic red alga bearing sex organs and tetrasporangia—a condition occurring in diverse Nemalionales (p. 625)—failed to undergo meiosis, the diploid carpospores would produce individuals which might at first bear both sex organs and tetrasporangia, the latter exhibiting reduction during spore-formation. If sexual fusion occurred in such diploid individuals, tetraploid forms would arise, and in this connection it is noteworthy that the majority of the investigated diplobiontic types have twice as many chromosomes as the haplobiontic ones ((347) p. 219). Further increases in chromosome-number may have been prevented by sexual sterility, so that the sex organs on the diploid (tetraploid ?) individuals became functionless and gradually aborted (cf. p. 724 and (771) p. 553).

C. THE DETAILED CLASSIFICATION OF FLORIDEAE

The following synopsis of the classification of Florideae is based on that proposed by Kylin ((387) p. 113, (389) p. 97; see also (400)). It is not possible to discuss earlier schemes of classification, nor do they, since the publication of the *Natürliche Pflanzenfamilien* (cf. also (587)), differ radically from that of Kylin, although there are numerous differences in matters of detail, largely as a result of more extended knowledge. It has not been thought advisable to include all the families, and a large number of genera have been omitted, but the opportunity is taken to give some details about additional genera, which were excluded from the previous treatment.

I. *Nemalionales:*

(*a*) Uniaxial forms:

1. *Acrochaetiaceae*: Acrochaetium, Kylinia, Rhodochorton.
2. *Batrachospermaceae*: Batrachospermum, Gulsonia, Nothocladus, Sirodotia.

The two Australian freshwater species of *Nothocladus* (644) possess an undulate thallus (fig. 297 C) in which the nodes tend to be obscured by abundant production of secondary laterals. The elongate axial cells

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(fig. 297 D, *a*) are not as wide as the cortical threads (*c*), which become laterally fused. The short laterals (fig. 297 E, *l*), arising from the cells of the curved carpogonial branches (*cb*), later fuse to form an envelope around the base of the carpogonium (fig. 297 G, *e*). The gonimoblasts (fig. 297 H, *g*) spread through the adjacent whorl and form carposporangia (*ca*) at or above the surface of the thallus.

The imperfectly known genus *Gulsonia*, described by Harvey ((273) p. 334, (278) p. 320; cf. also (599) p. 331) from South Australian seas, has a smooth cylindrical thallus, with a basic structure like that of *Batrachospermum*; the richly branched laterals unite distally to form a continuous small-celled surface-layer. The compact gonimoblasts have an envelope of sterile threads. Monosporangia are recorded, while Agardh ((10) p. 56) describes tetrasporangia.

3. *Lemaneaceae*: Lemanea, Tuomeya.
4. *Naccariaceae*: Atractophora, Naccaria.
5. *Bonnemaisoniaceae*: Asparagopsis, Bonnemaisonia.

(*b*) Multiaxial forms:

6. *Thoreaceae*: Nemalionopsis, Thorea.

Thorea ramosissima (16,290,464,581,588,596,731), only once recorded in the British Isles ((732) p. 428) but apparently not uncommon on the continent ((262) p. 307) and in other parts of the world, is usually found in swiftly running streams. The branched mucilaginous thalli are stated to reach a length of one metre and are densely covered with a felt of deeply pigmented hairs (fig. 297 A). The bulk of the thallus consists of irregularly intertwined hyaline threads (fig. 297 B, *me*) which, towards the outside, pursue a more longitudinal course and here bear densely arranged laterals. Some of these are elongate and project beyond the peripheral mucilage as the tomentum of hairs (*h*), which seems to be shed in the older parts. According to Schmitz ((596) p. 710; cf. also (464) p. 340, (581) p. 16) the threads composing the thallus are sympodially branched, each thread sooner or later terminating in a tuft of hairs, whilst longitudinal growth is continued by one or more laterals. There are evident pit-connections between the cells.

Certain peripheral branches bear swollen monosporangia (*sp*), which are the only reproductive organs known.[1] The germinating spores ((581) p. 20) give rise to a creeping one-layered basal stratum, which bears short, erect threads and *Chantransia*-like filaments, both of which can produce spores. In the mature plant several shoots arise from a basal disc which is encrusted with carbonate of lime and composed of a tangle of threads. A second species has recently been described from Jugoslavia (345).

Thorea has been regarded as a member of Phaeophyceae, but the presence of pit-connections and of starch-like granules in the cells ((464) p. 342) suggests a reference to Florideae. The thallus can be regarded as showing a specialised type of multiaxial structure.

[1] Schmidle's cystocarps ((581) p. 26) are probably epiphytic Blue-green Algae.

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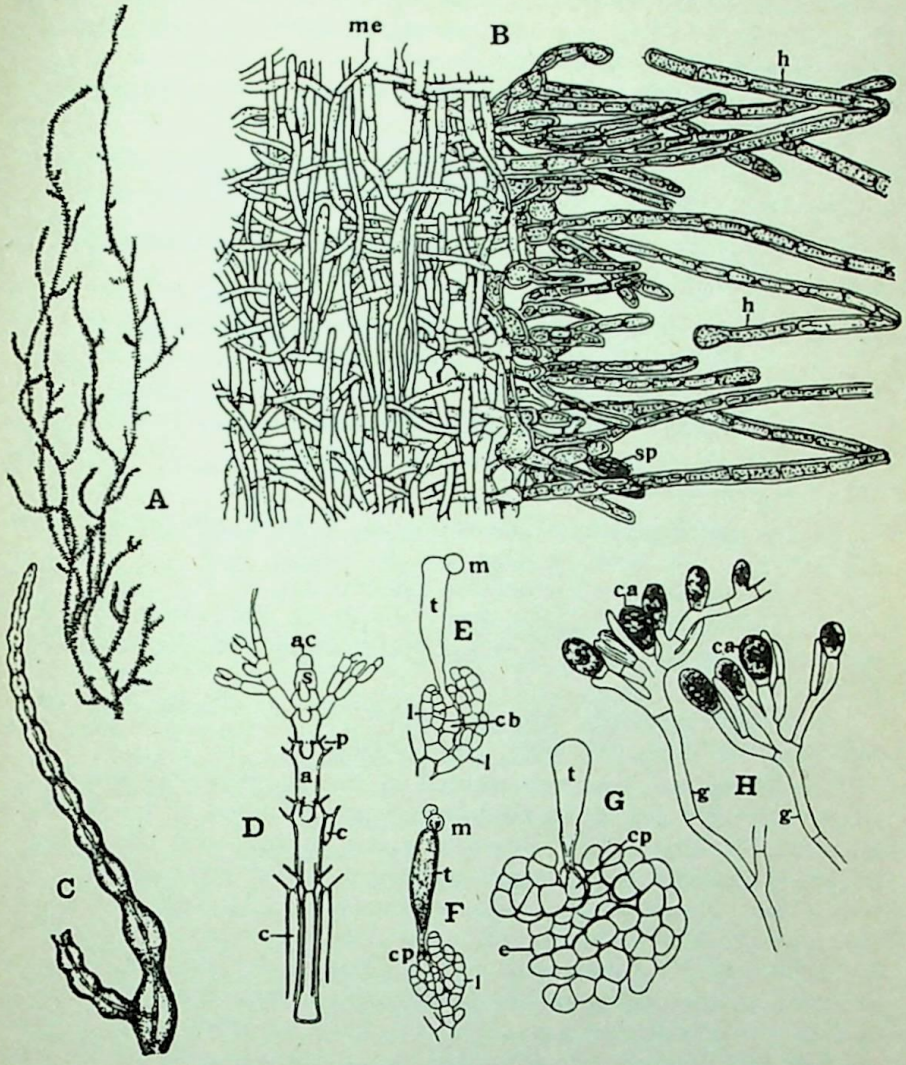

Fig. 297. A, B, *Thorea ramosissima* Bory; A, habit; B, part of thallus in longitudinal section. C–F, *Nothocladus nodosus* Skuja; C, part of a plant; D, apex of a branch, showing cortication; E, F, carpogonial branches. G, H, *N. tasmanicus* Skuja; G, developing fruit; H, gonimoblast-threads with carposporangia. *a*, axial cell; *ac*, apical cell; *c*, cortical threads; *ca*, carposporangia; *cb*, carpogonial branch; *cp*, carpogonium; *e*, envelope; *g*, gonimoblast; *h* (in B), hairs; *l*, lateral; *m*, spermatium; *me*, medulla; *p*, pericentral; *s*, segment; *sp*, monosporangium; *t*, trichogyne. (A after Schmitz; B after Hedgcock & Hunter; the rest after Skuja.)

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Nemalionopsis, recorded by Skuja (645) from the Philippines, is likewise found in fresh water. The little-branched cylindrical thalli possess a structure like that of *Nemalion*; hyphae are produced from the inner cortical cells. The only reproductive organs known are monosporangia borne terminally on the cortical threads.

Kylin ((400) p. 66) regards these two genera as a series parallel to the marine Helminthocladiaceae.

7. *Helminthocladiaceae*: Cumagloea, Dermonema, Dorella, Helminthocladia, Helminthora, Liagora, Nemalion, Trichogloea.

Dorella ((727) p. 205) is a diminutive unbranched form closely resembling *Nemalion*.

8. *Chaetangiaceae*: Chaetangium, Galaxaura, Scinaia.

II. *Gelidiales:*

1. *Gelidiaceae*: Gelidiella, Gelidium, Pterocladia.

III. *Cryptonemiales:*

1. *Gloeosiphoniaceae*: Gloeosiphonia, Schimmelmannia, Thuretella.

2. *Endocladiaceae*: Endocladia, Gloeopeltis.

3. *Callymeniaceae*: Callocolax, Callophyllis, Callymenia, Erythrophyllum ((11) p. 57, (709)), Euthora, Nereoginkgo, Rhizopogonia ((395) p. 6).

4. *Grateloupiaceae*: Aeodes, Cryptonemia, Grateloupia, Halymenia, Pachymenia, Prionitis, Thamnoclonium.

This family is mainly represented in the warmer seas and several genera (*Aeodes* ((4) p. 678), *Pachymenia*) are confined to the Southern Hemisphere. The Pacific *Prionitis* seems to lack the characteristic stellate medulla (p. 478) found in most of the other genera ((599) p. 513, (634) p. 20). *Cryptonemia Lomation* (Bertol.) J. Ag. (fig. 298 E) is a characteristic foliose form found in the Mediterranean. The sexual reproduction of *C. borealis* ((634) p. 16) is essentially like that of *Grateloupia*; both the carpogonial and auxiliary cell branches are lodged in cavities. In *Aeodes* ((383) p. 18) the product of fertilisation becomes invested by a definite wall, composed of numerous interlacing filaments. In *Cryptonemia* and *Prionitis* the tetrasporangia are formed in nemathecia.

5. *Dumontiaceae*: Acrosymphytum, Constantinea, Cryptosiphonia, Dilsea, Dudresnaya, Dumontia, Farlowia, Pikea, Thuretellopsis.

Farlowia and *Pikea* ((4) pp. 252, 262, (272) p. 246, (383) p. 15, (599) p. 519), which inhabit the western coasts of North America, have flattened distichously branched fronds, the central axis being particularly prominent in the latter; the carposporangia are embedded at the periphery of the medulla, in two longitudinal series on either side of the median line in *Pikea*, uniformly distributed over the cross-section in *Farlowia*.

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6. *Cruoriaceae*: Cruoria, Petrocelis.
7. *Rhizophyllidaceae*: Polyides, Rhizophyllis.
8. *Squamariaceae*: Coriophyllum, Cruoriopsis, Ethelia, Hildenbrandia, Peyssonnelia, Rhododermis.
9. *Corallinaceae*: Amphiroa, Archaeolithothamnion, Cheilosporum, Choreonema, Corallina, Epilithon, Lithophyllum, Lithothamnion, Melobesia, Phymatolithon, Porolithon, Sporolithon.

For other genera that have been distinguished, see (666) p. 257.

10. *Choreocolaceae*: Choreocolax, Harveyella.

IV. *Gigartinales:*

(*a*) Without procarps:

1. *Calosiphoniaceae*: Bertholdia, Calosiphonia.
2. *Nemastomaceae*: Nemastoma, Platoma, Schizymenia.
3. *Sebdeniaceae*: Sebdenia.
4. *Furcellariaceae*: Furcellaria, Halarachnion, Neurocaulon.

Families 1, 2, and 4 include the genera placed in Nemastomaceae by Schmitz (599).

5. *Solieriaceae*: Agardhiella, Anatheca, Eucheuma, Flahaultia, Meristotheca, Opuntiella, Sarcodiotheca, Solieria, Thysanocladia, Turnerella.

All these are multiaxial and most inhabit warmer seas. *Anatheca* and *Meristotheca* ((4) p. 582, (393) p. 25) are tropical foliose forms, distinguished by the occurrence of the carpogonial branches in small papillae borne on the surface of the thallus. *Sarcodiotheca* ((393) p. 15), based on the Pacific *Anatheca furcata* Setch. & Gardn. ((383) p. 36, (623) p. 310), lacks this feature. The cystocarps of all three resemble those of *Agardhiella* (p. 660), although in *Meristotheca* and *Sarcodiotheca* (fig. 298 A) the carposporangia (*ca*) are arranged in rows. In *Flahaultia appendiculata* Born. ((65) p. 278) the cystocarps are devoid of the peripheral fibrous investment.

Eucheuma ((2) p. 624, (50) p. 366, (727) p. 408, (729) p. 136, (753)), with species in the Indian Ocean and Japanese seas, has terete or flattened thalli, often occupied by abundant spiny branchlets which harbour the cystocarps. In *Thysanocladia* ((277) pl. 187, 211), an Australian genus with a flattened pinnately branched thallus, the carposporangia form rows radiating in all directions from a large branched (fusion ?) cell.

6. *Rissoellaceae*: Rissoella.
7. *Rhabdoniaceae*: Areschougia, Catenella, Erythroclonium, Rhabdonia.

All these are uniaxial. In *Areschougia* and *Rhabdonia*, most of the species of which are Australian, there is a three-sided apical cell, the segments of which produce only a single lateral ((393) p. 32); in the former the axial row remains prominent, while in *Rhabdonia* it is obscured by hyphae. The thallus of *Areschougia* ((277) pl. 13) is flattened with distichous branching, that of *Rhabdonia* ((141) p. 152, (277) pl. 152, 299) terete and radially branched. Apart from *Catenella* ((387) p. 66)

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the carpogonial branch is always three-celled. In the mature fruits there is always a large fusion-cell which, in *Rhabdonia* (fig. 298 D, *f*) and others, is directly connected with a cell of the axis (*a*).

(*b*) With procarps:

8. *Rhodophyllidaceae*: Acanthococcus, Calliblepharis, Craspedocarpus, Cystoclonium, Rhodophyllis, Wurdemannia(?).

Acanthococcus antarcticus Hook. & Harv. ((2) p. 434, (4) p. 34, (269) p. 477), with a flattened distichously branched thallus, is restricted to the Antarctic seas. A large fusion-cell is found in the mature gonimoblast (cf. *Cystoclonium*). *Craspedocarpus* ((393) p. 46, (599) p. 375; *Callophyllis erosa* Hook. & Harv. (274) p. 250) has a forked foliose thallus and resembles *Calliblepharis* and *Hypnea* in its reproduction; the fruits contain a fine-celled tissue (fig. 298 F, *s*) and several groups of carposporangia.

Wurdemannia ((272) p. 245) is an Atlantic genus of doubtful affinity, referred by some to the Gelidiales ((204) p. 544, (205) p. 136), by others ((53) p. 77; cf. also (599) p. 382) to the Rhodophyllidaceae. The habit (fig. 298 G) is like that of some species of *Gelidium*, but a single apical cell is not evident (cf. (50) p. 369); the branches tend to become joined by haptera (*h*). Zonate tetrasporangia are the only organs of reproduction known.

Families 5–8 include the majority of the genera placed in the Rhodophyllidaceae by Schmitz (599) who, however, referred *Calliblepharis* to his Sphaerococcaceae.

9. *Hypneaceae*: Hypnea.
10. *Plocamiaceae*: Plocamium.
11. *Sphaerococcaceae*: Heringia, Phacelocarpus, Sphaerococcus, Stenocladia.

Apart from *Sphaerococcus*, the genera of this family are confined to South Africa and Australia; they are probably all uniaxial. There is a large fusion-cell in the mature gonimoblast ((393) p. 48), while the fruits generally project markedly and are sometimes (*Phacelocarpus*) stalked. The tetrasporangia are cruciate.

12. *Gracilariaceae*: Ceratodictyon (Marchesettia), Curdiea, Gracilaria, Melanthalia, Tylotus.

Curdiea ((273) p. 333, (277) pl. 39) and *Tylotus* ((4) p. 428) are Australian seaweeds with foliose thalli, the latter with sporangial nemathecia. The cystocarp of *Tylotus* ((393) p. 59) is like that of *Gracilaria*. The tetrasporangia are cruciate.

Families 9, 11, and 12 are included in Schmitz's Sphaerococcaceae.

13. *Mychodeaceae*: Mychodea.
14. *Acrotylaceae*: Acrotylus ((2) p. 192), Hennedya.

These are multiaxial forms of the Southern Hemisphere, with zonate sporangia grouped in nemathecia and with cystocarps of a special type (fig. 260 D; cf. (393) p. 67).

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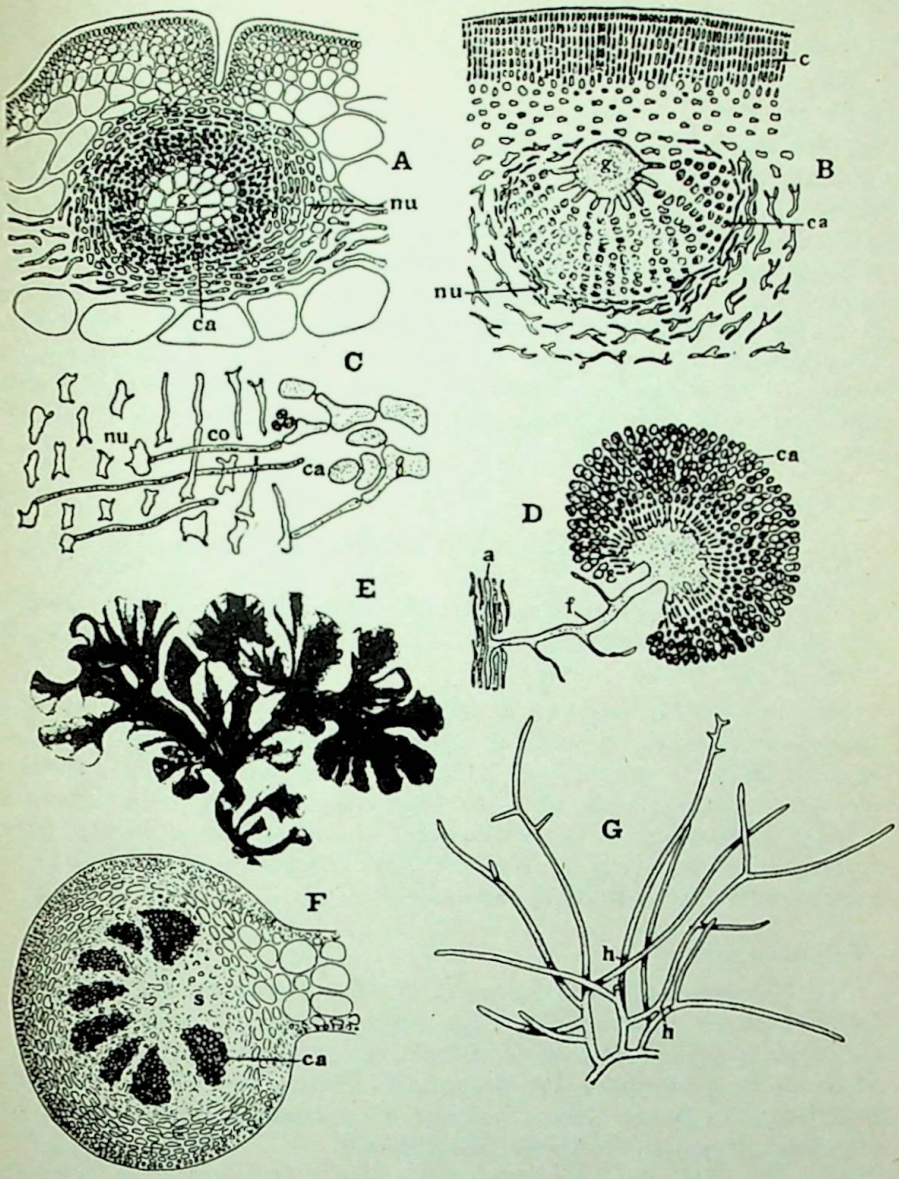

Fig. 298. A, *Sarcodiotheca furcata* (Setch. & Gardn.) Kyl., section of a young cystocarp. B, C, *Iridaea cordata* (Turn.) J. Ag.; B, section of a young cystocarp; C, connections (*co*) between gonimoblast and nutritive tissue (*nu*). D, *Rhabdonia verticillata* Harv., mature gonimoblast. E, *Cryptonemia Lomation* (Bertol.) J. Ag., habit. F, *Craspedocarpus erosus* (Hook. & Harv.) Schmitz, section of mature fruit. G, *Wurdemannia setacea* Harv., habit. *a*, axial cell; *c*, cortex; *ca*, carposporangia; *f*, fusion-cell; *g*, gonimoblast; *h*, haptera; *nu*, nutritive tissue; *s*, fine-celled tissue. (E after Kützing; G after Boergesen; the rest after Kylin.)

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15. *Phyllophoraceae*: Ahnfeltia, Ceratocolax, Gymnogongrus, Phyllophora, Stenogramma.

16. *Gigartinaceae*: Chondrus, Gigartina, Iridaea.

Iridaea (*Iridophycus* (626); cf. (404) p. 22, (775) p. 82) is mainly represented in the Southern Hemisphere ((269) pp. 188, 485), although some species occur on North Pacific coasts, being often found between tide-levels ((623) p. 298). The large, often unbranched, fronds commonly show iridescence. *I. cordata* J. Ag. (*I. laminarioides* Bory; *I. micans* Bory) is one of the largest of the Antarctic Florideae ((143) p. 149, (228) p. 54). The vegetative structure ((387) p. 45) is like that of *Chondrus*, but the threads composing the thallus always produce only two branches, as in *Endocladia* (p. 484); Kylin believes in an affinity between the two genera. The cells on the inner side of the gonimoblast of *Iridaea* produce numerous hyphae and constitute a nutritive tissue (fig. 298 B, *nu*), with which certain elements of the gonimoblast connect by means of elongate threads (fig. 298 C, *co*).

V. *Rhodymeniales:*

1. *Champiaceae*: Champia, Chylocladia, Coeloseira, Gastroclonium, Lomentaria.

2. *Rhodymeniaceae*: Bindera, Chrysimenia (sens. lat.), Coelarthrum, Dendrymenia, Epymenia, Fauchea, Gloeosaccion, Hymenocladia, Rhodymenia.

Epymenia ((274) p. 249, (277) pl. 89, (392) p. 22) bears its cystocarps and sporangia in small superficial outgrowths on the foliose thallus. *Hymenocladia* ((2) p. 772, (4) p. 311, (392) p. 24), most species of which are Australian ((277) pl. 20, 118), is distinguished by the abundant pinnate ramification of the thallus and the presence of short hyphae among the internal cells (cf. *Callophyllis*). The procarps and cystocarps are much like those of *Rhodymenia*.

VI. *Ceramiales:*

1. *Ceramiaceae*: Antithamnion, Ballia, Bornetia, Callithamnion, Carpoblepharis, Ceramium, Ceramothamnion, Compsothamnion, Crouania, Euptilota, Gattya, Griffithsia, Haloplegma, Halurus, Lejolisia, Microcladia, Monospora, Pleonosporium, Plumaria, Ptilocladia, Ptilota, Ptilothamnion, Reinboldiella, Seirospora, Spermothamnion, Sphondylothamnion, Spyridia, Vickersia, Wrangelia.

Ballia callitricha ((2) p. 74, (18), (267), (407) p. 400; incl. *B. Brunonis* Hook. & Harv. (269) p. 488) is a widely distributed ((405) p. 70) subantarctic and antarctic sublittoral form (see map 1, p. 8). The rigid threads show repeated pinnate branching (fig. 299 A), the older parts being densely corticated. In the rarer *B. scoparia* Harv. ((277) pl. 168) the branches are alternate.

Carpoblepharis, *Gattya*, and *Ptilocladia* show a modification of the batrachospermoid structure of *Crouania* and depart rather widely from other Ceramiaceae in habit. The first has species in South Africa and Japan, the other two are Australian. All three have flattened, pinnately

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branched thalli. In *Carpoblepharis* ((599) p. 500) and *Gattya* ((277) pl. 93, (599) p. 499) the axial cells bear whorls of six laterals, the branches of which unite to form a compact surface; in *Gattya* the inner cells of

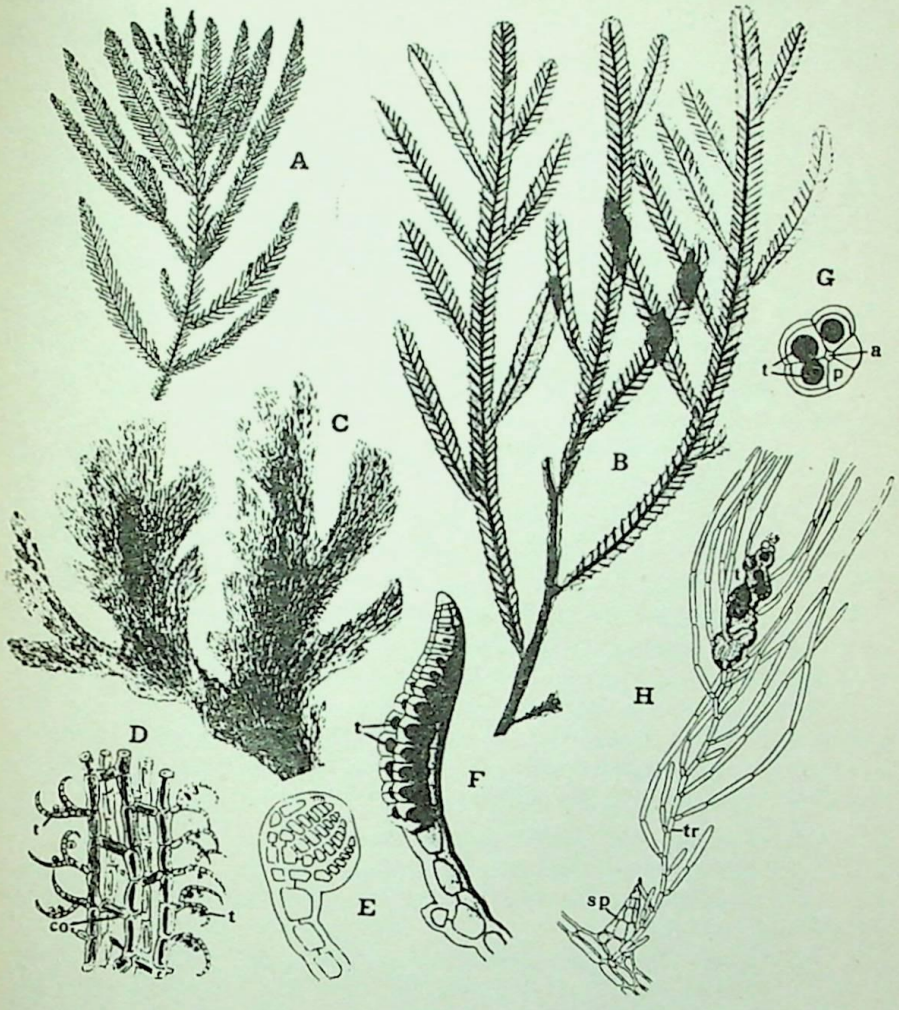

Fig. 299. A, *Ballia callitricha* (Ag.) Mont., habit. B, *Dictymenia Sonderi* Harv., part of a plant. C, D, *Haloplegma Preissii* Sond.; C, portion of a frond, natural size; D, small part of network, enlarged. E–G, *Colacopsis pulvinatum* (Schmitz) De Toni; E, older female frond; F, tetrasporangiate frond; G, transverse section of latter. H, *Wrightiella Tumanowiczii* (Gatty) Schmitz, part of a branch, with a spine (*sp*) and a fertile trichoblast. *a*, axial cell; *co*, cross-connections; *p*, pericentral; *t*, tetrasporangium; *tr*, trichoblast. (A after Kützing; E–G after Falkenberg; H after Boergesen; the rest after Harvey.)

the laterals are widely separated, giving a loose fistular structure. *Ptilocladia* ((277) pl. 209, (599) p. 499) has the laterals in whorls of four; in the older parts hyphae form an investment to the inner surface of the cortical region. Okamura (490) would unite *Reinboldiella* (see p. 528)

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with *Carpoblepharis*. The sporangia of the latter are confined to special fructifying shoots.

Haloplegma ((4) p. 89, (277) pl. 79, (599) p. 492), with species in the warmer seas, has a branched, spongy thallus (fig. 299 C), in which numerous *Callithamnion*-like threads are linked (fig. 299 D), by means of cross-connections (*co*), to form an elaborate network.

2. *Delesseriaceae:*

(*a*) *Delesserieae*: Apoglossum, Caloglossa, Claudea, Delesseria, Grinnellia, Hemineura, Hypoglossum, Membranoptera, Pantoneura, Vanvoorstia.

(*b*) *Nitophylleae*: Acrosorium, Cryptopleura, Gonimophyllum, Haraldia, Martensia, Myriogramme, Nitophyllum, Phycodrys, Polycoryne, Polyneura.

(*c*) *Sarcomenieae*: Cottoniella, Platysiphonia, Sarcomenia, Taenioma.

3. *Rhodomelaceae*: The following subdivision of this large family is based on Falkenberg (192):

(*a*) *Polysiphonieae*: Bryothamnion, Digenea, Polysiphonia, Stromatocarpus.

(*b*) *Lophothalieae*: Brongniartella, Doxodasya, Lophocladia, Lophothalia, Murrayella, Pteronia, Spirocladia, Wrightiella.

Wrightiella ((50) p. 310, (192) p. 559, (592) p. 222), found in the warmer parts of the Atlantic, resembles *Lophocladia* (p. 550) in the method of cortication and the endogenous origin of the lateral branches, most of which develop as spines of a soft consistency (fig. 299 H, *sp*), as well as in the production of sporangia (*t*) on the trichoblasts (*tr*). It is the upper part of the latter that becomes polysiphonous, the segments forming a single sporangium (fig. 299 H) and bearing a uniseriate branchlet. For *Spirocladia* see (56, 480).

(*c*) *Bostrychieae*: Bostrychia, Colacopsis.

(*d*) *Rhodomeleae*: Odonthalia, Rhodomela.

(*e*) *Chondrieae*: Acanthophora, Chondria, Coeloclonium, Herpochondria.

(*f*) *Laurencieae*: Janczewskia, Laurencia, Ricardia.

(*g*) *Pterosiphonieae*: Dictymenia, Pollexfenia, Pterosiphonia, Symphyocladia.

Dictymenia ((2) p. 1076, (6) p. 103, (192) p. 282, (270) pl. 7, (277) pl. 21), with species in the Indian Ocean and Australia, shows marked division of the pericentrals situated on the flanks of the principal axes and of the laterals. This results in a leafy expanse (fig. 299 B), in which axis and laterals appear as veins, while the free tips form projecting teeth; there is a narrow small-celled cortex. Trichoblasts, which do not bear the reproductive organs, occur only on the free tips.

(*h*) *Herposiphonieae*: Amplisiphonia, Dipterosiphonia, Herposiphonia, Periphykon, Placophora.

(*i*) *Lophosiphonieae* (see p. 566): Ctenosiphonia, Falkenbergiella, Lophosiphonia, Ophidocladus, Stictothamnion.

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(*j*) *Polyzonieae*: Cliftonaea, Euzoniella, Leveillea, Polyzonia.
(*k*) *Amansieae*: Amansia, Halopithys, Kützingia, Lenormandia, Osmundaria, Rytiphloea, Vidalia.

4. *Dasyaceae*: Colacodasya, Dasya, Dasyopsis, Dictyurus, Heterosiphonia, Thuretia.

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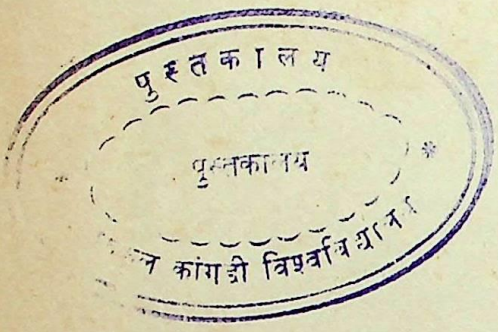

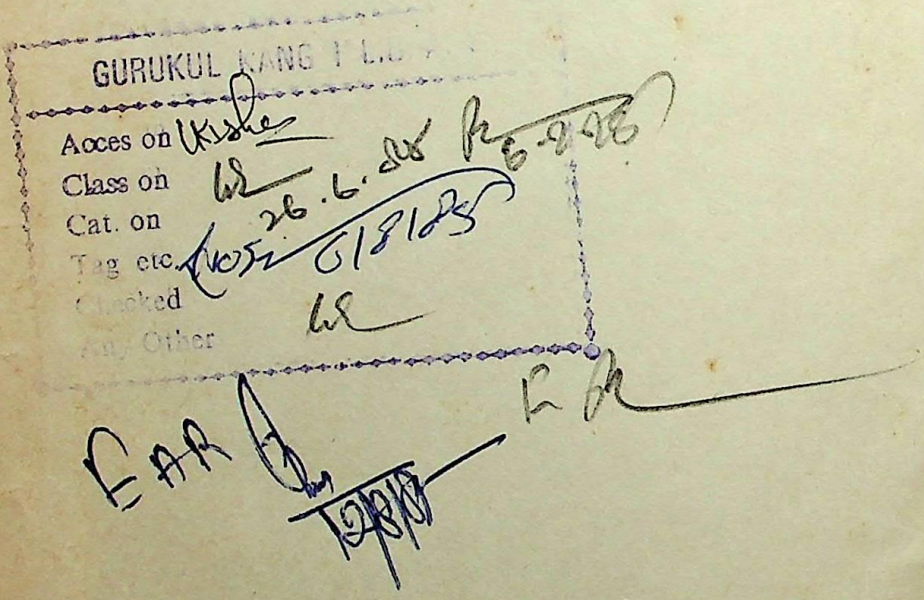

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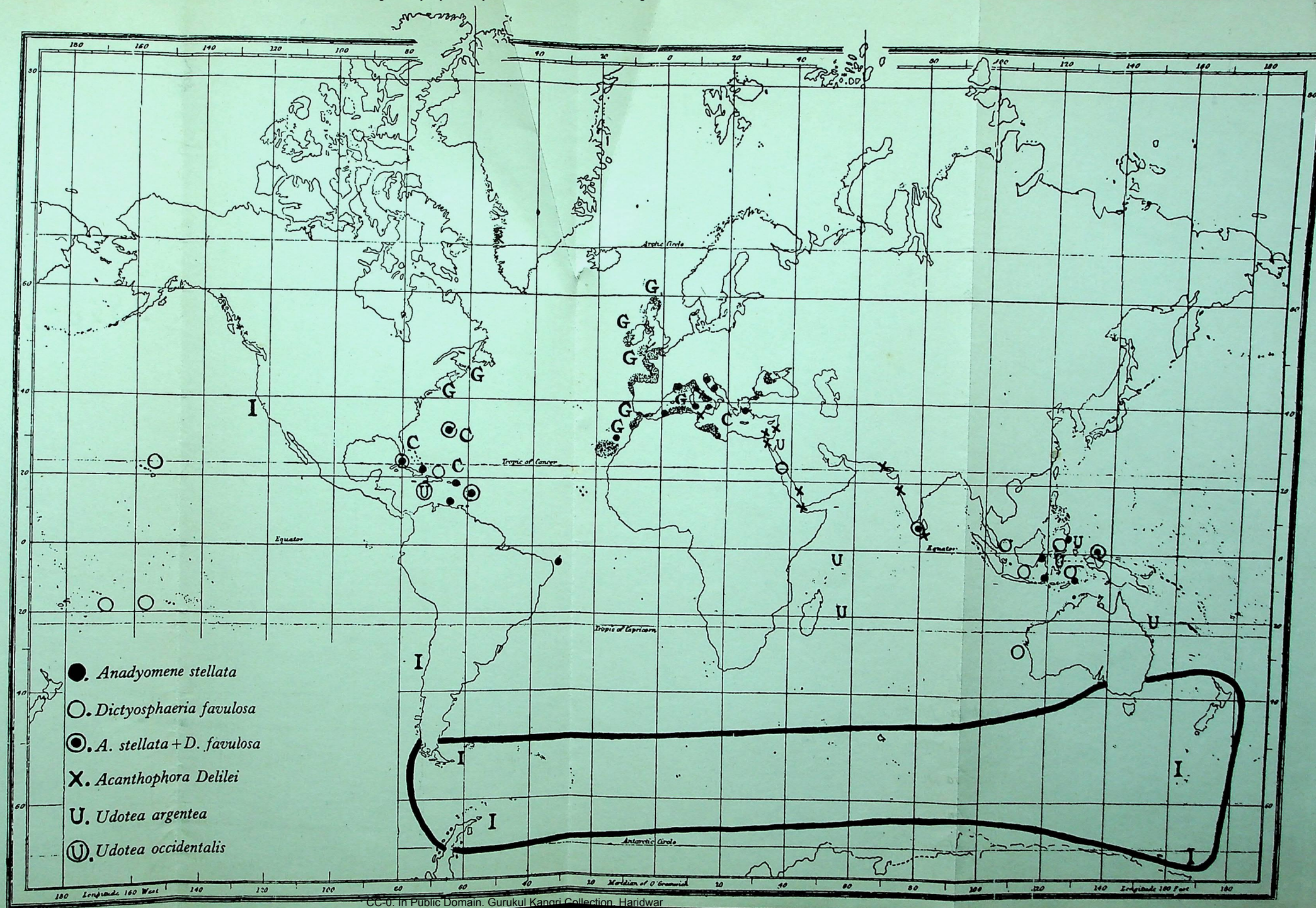

Map 1. Geographical Distribution of diverse Seaweeds (mainly after Svedelius and Feldmann). The continuous line in the Southern Hemisphere shows the area occupied by *Ballia callitricha* (Subantarctic); the dotted areas in the Northern Hemisphere the distribution of *Sphaerococcus coronopifolius* (Mediterranean-North Atlantic species). The map also shows the distribution of *Iridaea cordata* (I, Subantarctic, Western America), *Anadyomene stellata* (Indo-Pacific, Atlantic, Mediterranean), *Dictyosphaeria favulosa* (Indo-Pacific, Atlantic), *Caulerpa prolifera* (C, Mediterranean-tropical Atlantic), *Gymnogongrus norvegicus* (G, North Atlantic, Western Mediterranean), *Acanthophora Delilei* Lamour. (Mediterranean-Indian), and of the vicarious species *Udotea argentea* (Indo-Pacific) and *U. occidentalis* (Atlantic).

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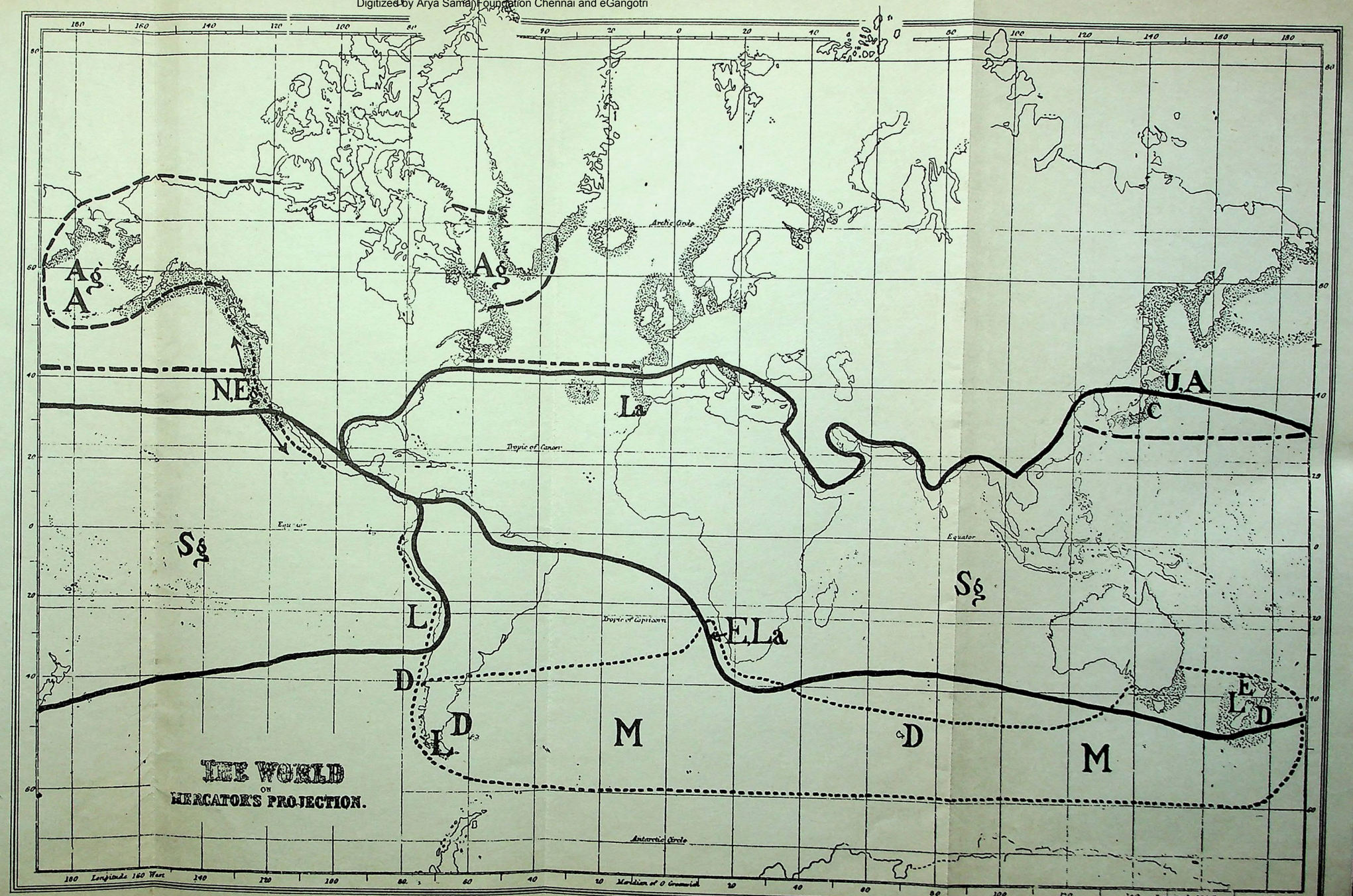

Map 2. Distribution of Laminariales and Fucales. The dots in the Northern Hemisphere show the area occupied by *Fucus*, in the Southern Hemisphere that occupied by the Australasian Fucales. The continuous line encloses the area occupied by the species of *Eusargassum* (*Sg*, after Setchell), the dotted line that occupied by *Macrocystis* (*M*), the interrupted line the area occupied by the Agareae (*Ag*); the line composed of dots and dashes shows the southern limit of Laminariales in the Northern Hemisphere. The distribution of the following is shown by letters: *A*, *Arthrothamnus*; *C*, *Coccophora*; *D*, *Durvillea*; *E*, *Ecklonia*; *Eg*, *Egregia*; *L*, *Lessonia*; *La*, *Laminaria* (outside the northern zone); *N*, *Nereocystis*; *U*, *Undaria*.

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